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THE ECOPHYSIOLOGY OF THE CAPE GROUND SQUIRREL

XERUS INAURIS (ZIMMERMANN)

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The ecophysiology of the Cape ground squirrel <u>Xerus</u> <u>inauris</u> (Zimmermann).

by

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The ecophysiology of the Cape ground squirrel <u>Xerus inauris</u> (Zimmermann).

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Abstract

Cape ground squirrels, <u>Xerus inauris,</u> are successful rodents of the southern African arid sub-region, living in burrows, exchanging the macro-climate for the micro-climate whenever the first becomes difficult. Several facets of their behaviour, thermoregulation, water balance and gut morphology were investigated and correlated with the climate and vegetation in the southern Kalahari. They are diurnal and live in social groups, raise altricial young, show signs of cooperative breeding, have female matriarchal systems and bachelor groups. The home range shapes were influenced by the dune topography of the study area. Although no specific evidence of gut specialization was found, they have a complex stomach, enlarged caecum and feed selectively on the most nutritious foodstuffs from a central place. The kidneys control water flux so that concentrated urine is excreted. <u>X. inauris</u> do not hibernate or estivate, but they do become hyperthermic during exposure to heat and show tendencies towards hypothermia when placed under low temperatures. Groups of squirrels huddle and bask during winter to counteract the cold, and during summer a parasol tail is used as a shading mechanism and excess heat is offloaded during sandbathing.

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AD   = apparent digestibility

C   = conductance

DEA   = digestible energy assimilation

EWL   = evaporative water loss

FEO   = faecal energy output

GEI   = gross energy intake

g   = gram

h   = hour

ha   = hectare

HCl   = hydrochloric acid

HTO   = tritium

J   = joule

kJ   = kilojoule

LBM   = lean body mass

l   = liter

m   = meter

ml   = milliliter

mm   = millimeter

NDF   = neutral detergent fibre

RMR   = resting metabolic rate

STP   = standard temperature and pressure

T_a = ambient temperature

T_b = body temperature

TBW   = total body water

TNZ   = thermal neutral zone

UEO   = urine energy output

VO_2 = oxygen consumption

WEI   = water economy index

CHAPTER 1

GENERAL INTRODUCTION

The Sciuridae (Gray 1837) comprise some 50 genera and 400 species found in diverse habitats throughout the world, with the exception of Australia, New Zealand, southern South America, the polar regions and dune desert like the Sahara. Squirrels were established in Eurasia and North America by the Miocene, after which time they invaded Africa. Because squirrels are relatively unspecialized, they evolved a wide variety of body forms and habits as adaptations to arboreal, semi-terrestrial, terrestrial, and semi-fossorial modes of life (Kingdon 1974). Squirrels have large eyes set in a small oval shaped head attached to a long cylindrical body and long tail. Members of the family have relatively primitive jaw muscles. Another primitive feature is the retention of one or two pre-molar teeth in each row. Teeth are simple, lacking the strongly projecting cusps or sharp ridges found in other rodents.

Moore (1959) described the eight genera occurring in Africa, of which four genera and six species are from the southern African subregion, except in association with the Namib desert. Two genera (Funisciurus and Paraxerus) are representative of the Tribe Funambulini, the African and Asian tree squirrels. The third genus, Xerus, is a member of the tribe Xerini, the African ground squirrels, while the fourth genus, Heliosciurus, the sun squirrels, belongs to the tribe Protoxerini (De Graaff 1981). The modern genera of Xerus and Paraxerus are known from the Laetolil Beds and the Ndolanya Beds, Tanzania (Denys 1983) and at Olduvai, Tanzania and could be dated as far back as from the early Miocene (Lavocat 1978).

The tribe Xerini include monotypic species (X. inauris and X. princeps) occurring in southern Africa, while two other species of Xerus are found outside the subregion, with X. rutilus found in north-east Africa and X. erythropus ranging from Senegal, Sudan and into south western Kenya (Kingdon 1974). The Cape ground squirrel, first called Sciurus inauris and later X. inauris, was first mentioned by Pennat in 1780 and then described by Zimmermann (Sclater 1901). The generic name is derived from the Greek xeres meaning dry and inauris meaning no ear from Latin, in reference to the very small pinnae. Xerus inauris as named by Meester, Davis & Coetzee (1964), was reported by Zeally (1916) as a fossil from the upper Pleistocene found near Bulawayo. Apart from this discovery, no other fossil specimens have been found in southern Africa (De Graaff 1981).

X. inauris occurs in the South West Arid Zone, found specifically in the Orange Free State (O.F.S.) to the northwestern and northeastern Cape Province into Namaqualand and Namibia. From the western Transvaal it ranges northwards into Botswana and the central and southwestern Kalahari (Sclater 1901, Shortridge 1934, Lynch 1975, Smithers 1971), where a mean annual rainfall of 100 to 500 mm prevails. Nonetheless, the species has been recorded in wetter parts of the O.F.S. receiving up to 750 mm.

Distribution and general biology of the species has been described by earlier workers such as Snyman (1940), Ewer (1966), Zumpt (1968; 1970), Smithers (1971), Lynch (1975) and Stewart (1975). More recently Straschil (1974, 1975) and Hertzig-Straschil (1978, 1979) described behaviour patterns and biology of ground squirrels, and Robinson, Skinner & Haim (1986) investigated the species status of X. princeps. The first data on thermoregulation in X. inauris were published by Bowling (1958, 1959), which was followed by Haim, Skinner & Robinson (1987) examining the bioenergetics and urine production of acclimated Xerus. Marsh, Louw & Berry (1978) reported on kidney function. In addition, the use of the tail as a parasol and thermoregulatory device was

investigated by Bennett, Huey, John-Adler & Nagy (1984) and further discussed by Van Heerden & Dauth (1987).

Motivation for this study

X. inauris are large, diurnal, burrowing, herbivorous and colonial rodents. Their distribution in semi-desert areas of low, unpredictable rainfall poses several questions concerning adaptations for survival. Animals that possess elaborate and efficient physiological adaptations and possibly behavioural mechanisms, predominantly inhabit xeric environments (Louw & Seely 1982). This suggests that such animals will, at some stage or another, make full use of their capabilities and the question can be asked : how 'stressed' are these squirrels in what we, as humans, perceive as a stressful environment? X. inauris found in the Kalahari is the only diurnal species with a mass of approximately 650 g playing a role in the foodweb as primary consumer, taking mainly herbage and taking a siesta during the wa

rmest part of the day. Therefore, X. inauris has to reduce the overall thermal demands for such a lifestyle. It can be hypothesised that their penetration into the arid environment is facilitated by a larger body size. Being large could give these animals greater thermal inertia, and a relatively smaller surface to volume ratio and this could have an influence on insulation and conductance. Furthermore, a larger size could improve the possible escape from many small predators.

Arid environments are relatively similar throughout the world, being characterised by limited water, large fluctuations in daily temperature and seasonal and erratic rainfall. Similar selective pressures in different semi-desert areas could therefore be expected. For instance, Antelope ground squirrels Ammospermophilus leucurus of the Mojave Desert, were found to be active for 12 h daily throughout the year, but managed this by adapting to an energetically

conservative lifestyle, expending lower than predicted amounts of water and having low metabolic rates (Karasov 1981, 1983b). Similarly it could be expected that X. inauris would lower their metabolism, body temperature and water flux. Moreover, that these factors, digestion and behaviour play intricately interwoven conservation roles to make this 'stressed' semi-desert situation of extremes easier. One of the major mechanisms by which body temperature is controlled is the re-distribution of blood, from the centre to the periphery of the body in warm conditions, or withdrawal from the periphery to more central regions in cold conditions. This process of altering skin temperature, will alter the heat available for removal from three non-evaporative routes. These could include pilo-erection (raising of hairs); the engorgement or vasorestriction of superficial veins of limbs and thermal insulation; behavioural control, including the alteration of posture and huddling, is a further means of altering heat exchange as is escape into other microclimates such as burrows. Insulation outside the skin can provide an air-layer trapped by the interstices of the fur and furthermore, by the the shading capacity of the parasol tail. All these adaptations to ambient temperature could be enhanced by enlarging body size.

X. inauris could have adjusted behaviourally and by greater or lesser heat production, to the annual cycle of climatic variation. Dry tropical climates are suitable for homeotherms provided that the water supply is adequate, and this supply would possibly be ensured by water obtained from food as well as efficient water conservation mechanisms. It is hypothesised that X. inauris survived 20 million years on the continent of Africa and as a living fossil could do so because of: effective avoidance of temperature extremes and living as colonial huddlers; the capacious caeca with commensal populations of bacteria which break down cellulose; the possibility that the stomach could be used as a temporary storage organ when food has to be eaten in large amounts in short spurts of time; and that water is conserved by effective kidney function.

Many other factors could enable X. inauris to interact successfully with the climatic extremes of the macro and micro environment. Factors such as living

in social groups, raising altricial young, showing signs of cooperative breeding, female matriarchal systems, male bachelor groups, selective feeding, central place foraging, basking, sandbathing, parasol tail usage, no hibernation or estivation, all of which instigated a desire to study X. inauris. Several facets of behaviour, thermoregulation, gut morphology and water balance were investigated in conjunction with the climate and vegetation of the southern Kalahari semi-arid savannah.

CHAPTER 2

STUDY AREA

A. DESCRIPTION

The study was conducted in the Kalahari Gemsbok National Park, Cape Province, South Africa. X. inauris study groups were located in the Nossob riverbed and adjacent dunes, in the vicinity of Nossob camp (25° 25' S and 20° 36' E).

The area is dominated by dunes underlined with a substrate of calcareous sandstone which is exposed in the open wide riverbeds, pans and incipient pans (braks) (Leistner 1967). The aeolian sands are derived from rocks occurring within the Kalahari basin itself during the Tertiary, being redistributed during the Pleistocene by wind and water. No distinct soil horizons occur. The sands could be divided into white, pink and red sands. X. inauris prefer to burrow in open terrain with harder surfaces as found in riverbeds, pans, incipient pans and dune streets.

The vegetation is characteristically Kalahari thornveld (Acocks 1953). Several Acacia species such as A. erioloba, A. haematoxylon, A. mellifera and A. hebeclada as well as Albizia anthemintica, Grewia flava, and Boscia albitrunca are the most abundant trees and shrubs. Grasses such as Eragrostis lehmaniana, Stipagrostis amabilis, Centropoda glauca, Schmidtia kalahariensis, Stipagrostis obtusa and Stipagrostis uniplumis cover the dunes and alluvial riversides and when enough rain falls, extensive stands of Panicum coloratum and Eragrostis bicolor are found in the riverbeds.

B. RAINFALL

Louw & Seely (1982) described the Kalahari as an interior continental 'desert' positioned between major wind belts and associated storm belts.

Table 1. Annual rainfall (mm) measured between January 1984 and December 1989 at Nossob camp in the Kalahari Gemsbok National Park .

MONTH	YEAR					
	84	85	86	87	88	89
JAN	2,2	29,7	7,4	9,3	55,8	76,8
FEB	1,9	10,0	9,7	85,5	63,5	92,0
MAR	21,8	29,9	11,9	2,5	32,1	6,3
APR	82,6	1,3	9,1	3,6	95,4	33,8
MAY	9,1					
JUN			6,1			
JUL			3,7	0,2		
AUG						
SEP			0,4	1,7		0,2
OCT	21,9	5,0	8,4	6,5	6,5	
NOV	32,3	5,5	65,6	46,4	20,5	2,5
DEC		51,9	3,4	10,8	58,7	
TOTAL	171,8	133,3	125,7	168,5	332,5	211,3

Although a friction layer of 7,5 cm above the surface is described as windless (Leistner 1967), wind is a common phenomenon. Sand storms do occur intermittently for approximately eight to 14 days during August, September and October, causing no drastic physical geological changes. A dominant north wind is usually hot, while a south wind is associated with cold weather. Rainfall in the form of convective storms, generally precipitates between October and

April, occurs in scattered storms in time and space. Localised showers occur, as evidenced by patchy green vegetation during drought years.

While the mean annual rainfall measured during the past six years was 190,5 ± 76 mm of rain, the period embraced three years of drought (that is a period with less than 20 % of the average rainfall) between 1983 and 1987 (Table 1). During those summers an average precipitation of 143,6 ± 25,0 mm was recorded. Single showers of less than 10 mm of rain seemed ineffective in producing any sprouting vegetation, unless followed within a two weeks by another storm in excess of 10mm (Leistner 1967).

C. TEMPERATURES

Kalahari temperatures fluctuated considerably during the present study, and the region can be described as one of the hottest and coldest in South Africa. Leistner (1967) described the Kalahari year as having mainly two seasons: summer and winter being dictated by sharp and sudden ambient temperature changes. He did however define two periods during the summer: hot-wet and hot-dry but only one for the winter: the cold-dry season. During January, the hottests month of the year, mean daily maximum and minimum temperatures of 36,6 ± 1,5 ° C and 19,8 ± 1,5° C respectively have been recorded (Table 2). Soil surface temperatures can rise to 70° C in summer. Most winter nights are cloudless and the mean frost period lasts for 98 days. During July, the coldest month of the year, mean daily maximum and minimum temperatures of 22,8 ± 0,6° C and -0,11 ± 1,2° C have been measured respectively. It can be expected that when small mammals experience cold weather they go into states of hibernation or temporary torpor, escape, piloerection, huddling and basking. During hot weather the result could be the opposite and radiation, especially short-waves, are reflected from sandy surfaces onto plants and animals. The absorption of these rays may add to metabolic heat and consequently a chain

reaction may follow; conduction; convection; evaporation, escape, orientation, reflectance, hyperthermia and even estivation.

Table 2. Average ambient maximum and minimum temperatures measured from January 1988- December 1988 at Nossob camp in the Kalahari Gemsbok National Park.

MONTH	MAXIMUM °C	MINIMUM °C
JAN	36,6 ± 1,5	19,8 ± 1,5
FEB	33,5 ± 2,5	19,6 ± 1,9
MAR	33,5 ± 0,6	16,9 ± 1,8
APR	29,4 ± 1,9	11,9 ± 1,3
MAY	26,3 ± 1,8	5,9 ± 2.4
JUN	22,4 ± 0,9	1,1 ± 1,7
JUL	22,8 ± 0,6	-0,1 ± 1,2
AUG	26,3 ± 1,1	3,4 ± 1,5
SEP	28,4 ± 1,2	8,0 ± 2,3
OCT	31,4 ± 1,6	13,5 ± 2,3
NOV	33,7 ± 0,9	16,3 ± 1,8
DEC	35,7 ± 2,1	19,4 ± 2,4

D. MAP OF BEHAVIOURAL STUDY AREA

The behavioural study area known as 'Rodent Hill', covered an area of 500 m^2 and centred in an incipient pan, which was surrounded by large red dunes,

shaping the edge of the study area like a cone. Within the study area, mapped with a compass (calibrated equipment) and tape measure, 53 burrows were mapped as well as all bushes and trees (Fig. 1A and 1B).
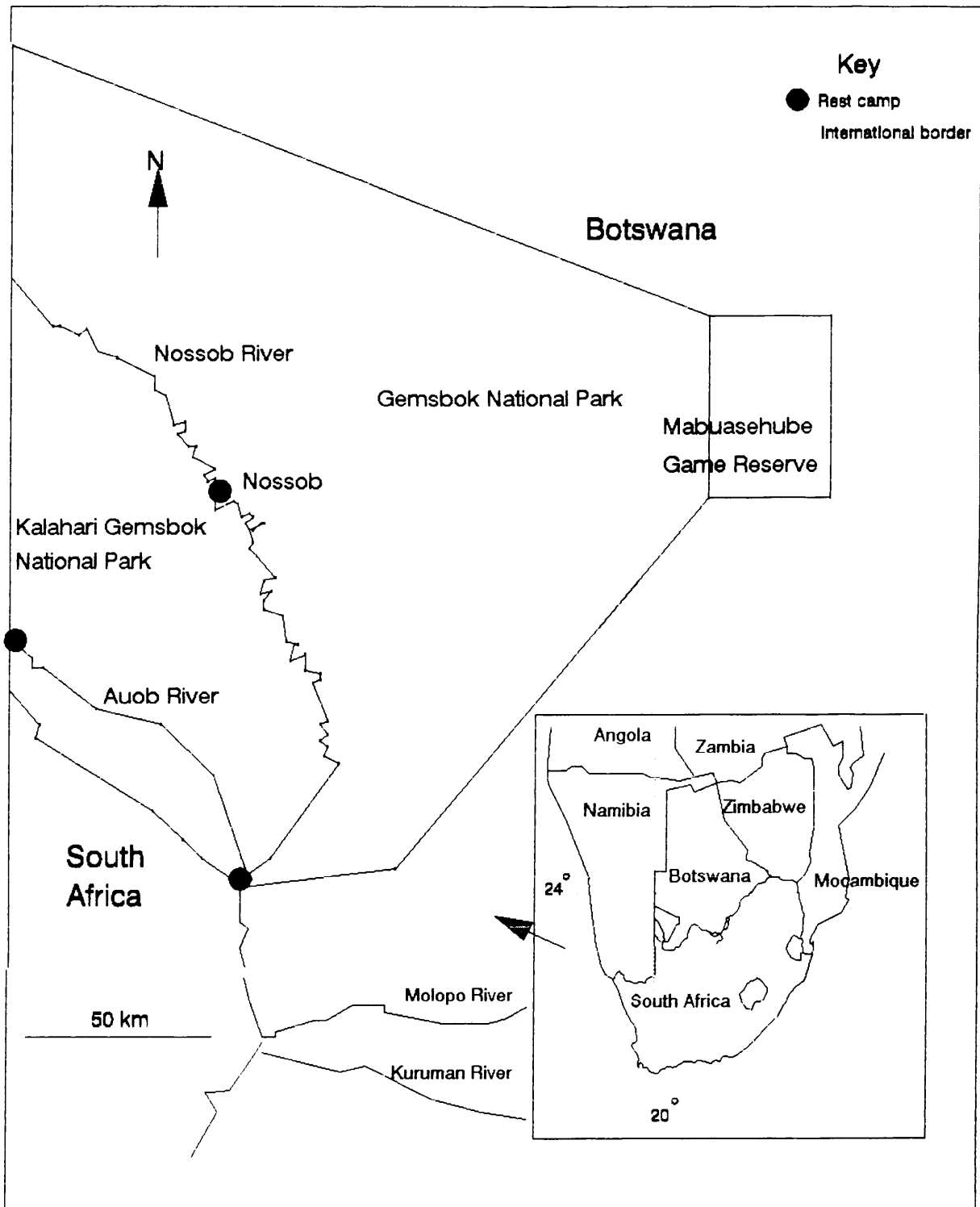
Fig. 1A. The southern Kalahari, showing the Kalahari Gemsbok National Park, Gemsbok National Park and the study area.
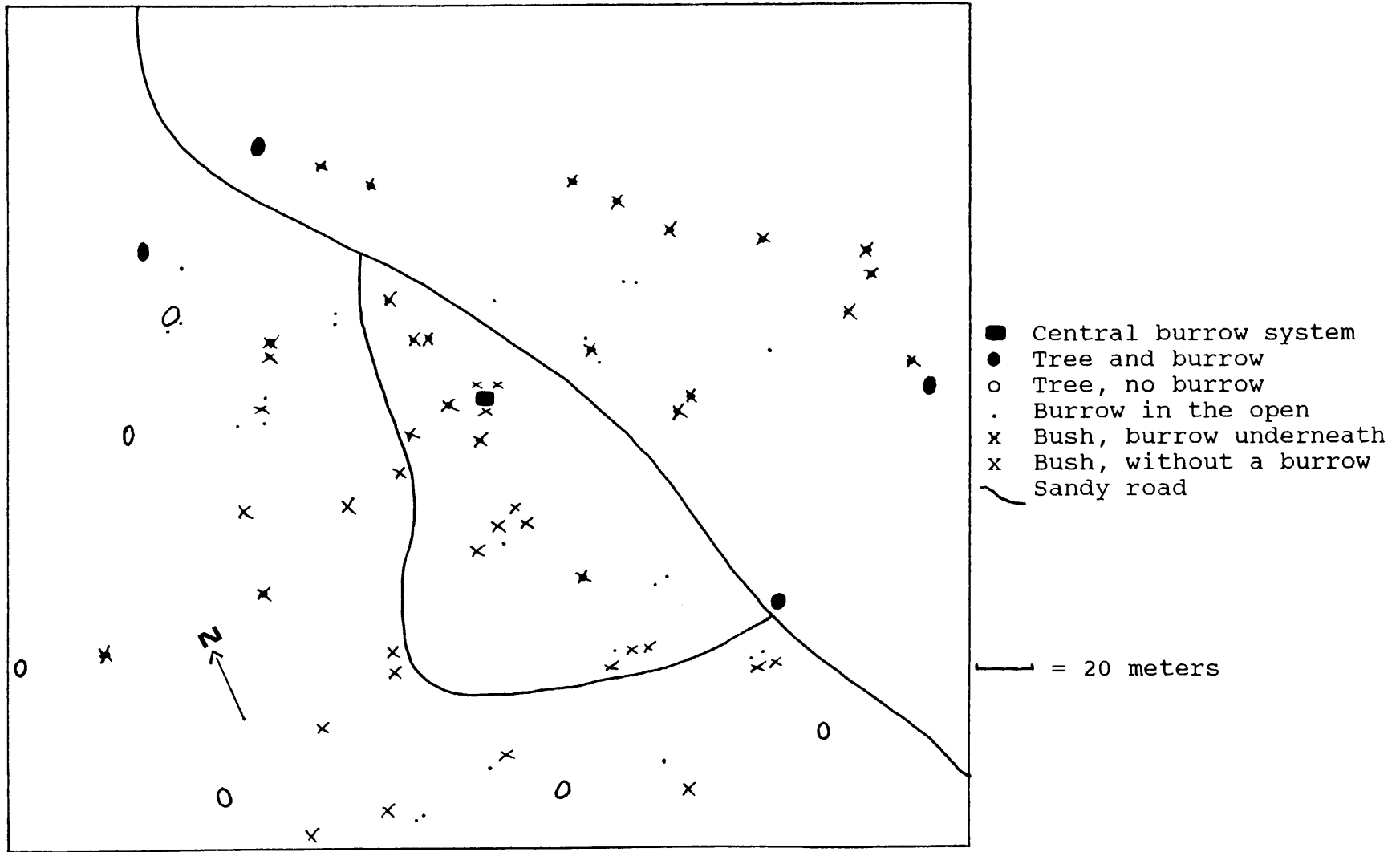
Fig. 1B. Map of the study area, Rodent Hill.

Legend:
- ■ Central burrow system
- ● Tree and burrow
- o Tree, no burrow
- . Burrow in the open
- x Bush, burrow underneath
- x Bush, without a burrow
- Sandy road

⊢—⊣ = 20 meters

E. TIME SCHEDULE

The time-schedule of the study is summarized in Table 3. The behavioural part of the study commenced during August 1987 and was completed during June 1988. The physiological experimentation was accomplished during several short periods in the field and university laboratory.

Table 3. Time-schedule of the study of X. inauris, undertaken from 1987 until 1990.

MONTHS	YEAR			
	1987	1988	1989	1990
JAN	Single therm	Behaviour	Water flux lab	Field water flux
FEB		Behaviour		Lab flux results
MAR	Plant quads	Behaviour		
APR	Plant H$_2$O	Behaviour	Analyses data	
MAY		Behaviour	Analyses	
JUN	Single thermo	Behaviour	Analyses	
JUL	Huddling experiment	Field water flux		
AUG	Behaviour	Huddling experiment	Field water flux	
SEP	Behaviour	Plant H$_2$O	Water flux lab	
OCT	Behaviour			
NOV	Behaviour Plant quads	Histology of the gut	Plant quads	
DEC	Field water flux	Morphology of the gut		

CHAPTER   3

LIFE   HISTORY

Published   scientific   and   popular   accounts   of   squirrels   have   dealt   with   many   phases   of   their   life   history.   These   studies   together   with   information   from   personal   observations   are   presented   to   aid   in   the   interpretation   of   the   behavioural   and   physiological   dynamics   of   the   chapters   to   follow.

A. FEEDING   HABITS

Herzig-Straschil   (1979)   reported   that   ground   squirrels   fed   mainly   on   dry   vegetable   matter   during   the   winter   months,   switching   to   fruit,   seeds,   grass,   stems   and   bulbs   in summer.   Zumpt   (1970)   reported   from   stomach   analysis   that   insects   were   taken,   but   Marsh   et al.   (1978)   found   none   in   stomachs   from   squirrels   in   the   Etosha   National   Park,   Namibia.   Here   they   reported   them   as   being   entirely   herbivorous,   taking   grasses   during   the wet season   and   switching   to   underground   plant   storage   organs   in   the   dry   season.   In   the   Kalahari   the   question   then   arose: what was   available   to   feed   on   and   how   do   X. inauris   satisfy   their   nutritional   needs?

Methods

To   monitor   plant   production   (that   is   the   average   dry   mass   produced   per   season),   two   sites   were   selected   and   monitored   during   the   day time.   One   of   these   was   at   the   study   site   :' Rodent   Hill'   and   the   other   at a random   site   in   the   vicinity   of   the   study   site   'A. haem'   in a dominant   A. haematoxylon   veldtype.   At   the   A. haem   site   a   25   m^2 exclosure   was   erected.   Wire   quadrants   of   1m^2 were   systematically   positioned   at   both   sites during   March   and   November   1987.   The

following were recorded within each quadrant : 1. Species composition of grass and forbs, using the dry rank method (t'Mannetje & Haydock 1979) 2. Grasses and forbs were clipped to just above ground level and weighed. After drying samples to constant mass at $60°$ C in a drying oven, the dry weight was calculated. Dry samples of 0,5 g were then analysed for protein following the Kjeldahl method (Horwitz 1970) and fibre following Van Soest (1964). Although in the present study the precise selection of plant species and parts at a given time was not estimated in order to define frequency of feeding, daily observations provided enough proof to give details on preferred species. After careful daily observation of squirrel feeding habits especially during the days during the behaviour study, a list of preferred species for every season could be listed. Energetic values for the three preferred main grass species (Eragrostis lehmaniana; Stipagrostis kalahariensis; and Stipagrostis amabilis) and samples of Dipcadi glaucum bulbs and Grewia flava berries were determined after collection during September 1987, December 1987, February 1988 and June 1988, using an adiabatic CP 400 calorimeter (Gallenkamp). Benzoic acid with an energy content of 26,43 kJ/g was used as a standard.

At the 'Rodent Hill' study site, a permanent transect line was marked in the same way as in the nearby exclosure. The boot-tip method (Bond, Ferguson & Forsyth 1980) was used to determine basal and canopy cover, moribund and bare ground. During early mornings, wire quadrants of 50 cm^2 were also placed randomly (n = 10) in the squirrel habitat at 'Rodent Hill' during the behavioural study period and the plants covering these quadrants were removed, identified and weighed and water content assessed. The soil inside the quadrants was then removed to a depth of 20 cm (squirrels do not dig deeper for their food) and sifted to collect root and bulb material. This was also weighed and dried. All these samples were weighed with a Passola balance to the nearest 0,5 g.

Results and discussion

At Rodent Hill the percentage plant cover increased with rainfall ($y= 13.23 + 0.24x$; $r=0.92$; $df = 14$). The percentage cover of each species identified when walking the transect is listed (Appendix 1). S. kalahariensis, E. lehmaniana and Tribulus terrestris were the dominant species available all year round. The average percentage cover of vegetation was lowest during the cold dry winter (August) and early summer (hot-dry; September, October) when little rain fell. Other plants of importance are annual species such as catstail (Herbstaedia sp.), skaapbossie (Pentzia sp.) and the brandboontjie (Sesamum sp.) sprouting after the first summer rains and available every year and consumed by X. inauris. G. flava, A. mellifera, and A. haematoxylon were most important in providing shade and as locations of burrow sites. Numerous A. erioloba trees were also found in the area (Fig. 1B).

Table 4. Available plants observed consumed by X. inauris between August 1987 and July 1988.

Annual plant species available	
Plant species	Portion consumed
Eragrostis lehmaniana	l, sh
Stipagrostis kalahariensis	l, sh
Stipagrostis amabalis	l, sh
Grewia flava	fr
Tribulus terrestris	l, fl, r
Helichrysum agyrosphaerum	l, fl
Limeum myosotis	l, fl, r
Herbstaedia linearis	l
Indigofera agyroides	l, fl
Sesamum triphyllum	fl
Citrillus lanatus	l, fl, fr, ru, r
Dipcadi glaucum	bu

* l=leaves, sh=sheaths, fr=fruits, fl=flowers, r=roots, ru=runners, bu=bulbs.

From Appendix 1 it is apparent that the % cover depended on the rainfall and some plant species were more prolific during summer than winter. X. inauris would take the best grasses or roots that were available even if it meant extensive digging during the winter months (Chapter 4).

In Table 4 the available plant species consumed and preferred by X. inauris throughout the behavioural study year are listed. The dietary shift between seasons is reflected in the marked seasonality of particular foods such as G. flava berries and the Tsama melon fruit (Citrullus lanatus). Seasonal differences in feeding response could be due to chemical changes in the food, the availability of alternative foods, or changes in feeding preferences related to reproduction or water availability (Appendix 1).

During summer the leaves and sheaths of certain grasses such as S. kalahariensis and E. lehmaniana were predominantly taken. Annuals such as Limeum and T. terrestris leaves, stems and flowers were eaten together with Sesamum leaves and flowers. The fruits and runners of the Tsama were taken whenever available but only after some other animal such as a gemsbok (Oryx gazella) had opened the former. In the winter months, grasses (particularly the leaf blades and growth points of stems) such as S. kalahariensis and E. lehmaniana, although half-green in colour and showing signs of 'senescence' were still eaten. Species that were completely brown and desiccated were avoided, flowers of the winter ephemeral Helichrysum sp. were eaten and squirrels resorted to digging bulbs such as D. glaucum. Berries of G. flava which are high in water and protein content became a very important food resource during May and June. X. inauris have been reported to be poor climbers (Smithers 1983) but during the present study they were found to climb G. flava bushes with ease to retrieve berries. These berries (Fig. 2A, B & C) contain up to 17 % protein and 60 % water during the winter months. The 'naba' fungus occurring near the roots of S. uniplumis and S. ciliata was also eaten during June. Similarly the hypogeous fungus Rhizopogon sp. was found to be a major

food source for golden-mantled squirrels (Spermophilus saturatus) during the summer months (Kenagy, Sharbaugh & Nagy 1989).

Cape ground squirrels would select plant parts as other herbivores do (Janzen 1979, Milton 1979). The nutritional value of plant resources for X. inauris depended on what plant tissues were eaten and when they were taken. In Figure 2 the leaf, water and protein content of certain species are shown together with their variation over a period of one year. From the seasonal collection of preferred plants and their parts, the significance of seasonal changes for ground squirrel nutritional ecology could be assessed. Leaf and water contents of preferred plant species were highest during the early (hot-dry) and late summer (hot-wet) months, in conjunction with rainfall, when optimum growth for many Kalahari plant species occurred (Fig. 2). Plant species such as E. lehmaniana and T. terrestris, provided succulent leaves, stems, flowers and roots throughout the year. Such plant material served as a water source for X. inauris during the summer and roots of T. terrestris and D. glaucum as a water source during the winter. The mineral requirements of X. inauris have not been determined. However several authors have reported osteophagia and geophagia in other squirrel species (Havera & Smith 1979, Karasov 1985), such behaviour, however, was never observed for X. inauris.

When the protein content of leaves, roots and berries increased during the hot-wet summer, the fibre content decreased (y= 82,48 + -2,01x; r=0,92; df=20; P<0,05). Whenever protein levels of preferred food items declined, X. inauris changed their diet to other plant species with a higher protein and water content (Fig. 2).

The fibre content (NDF=neutral detergent fibre) of plant leaves increased significantly (y= 80,62 + -0,58; r=0,60; df=20; P<0,05) when water content decreased (Fig. 2). Leaves contained more indigestible structural carbohydrates and less protein and water with advanced maturity, while seeds often contained higher energy nutritive elements than the leaves of the parent plant.
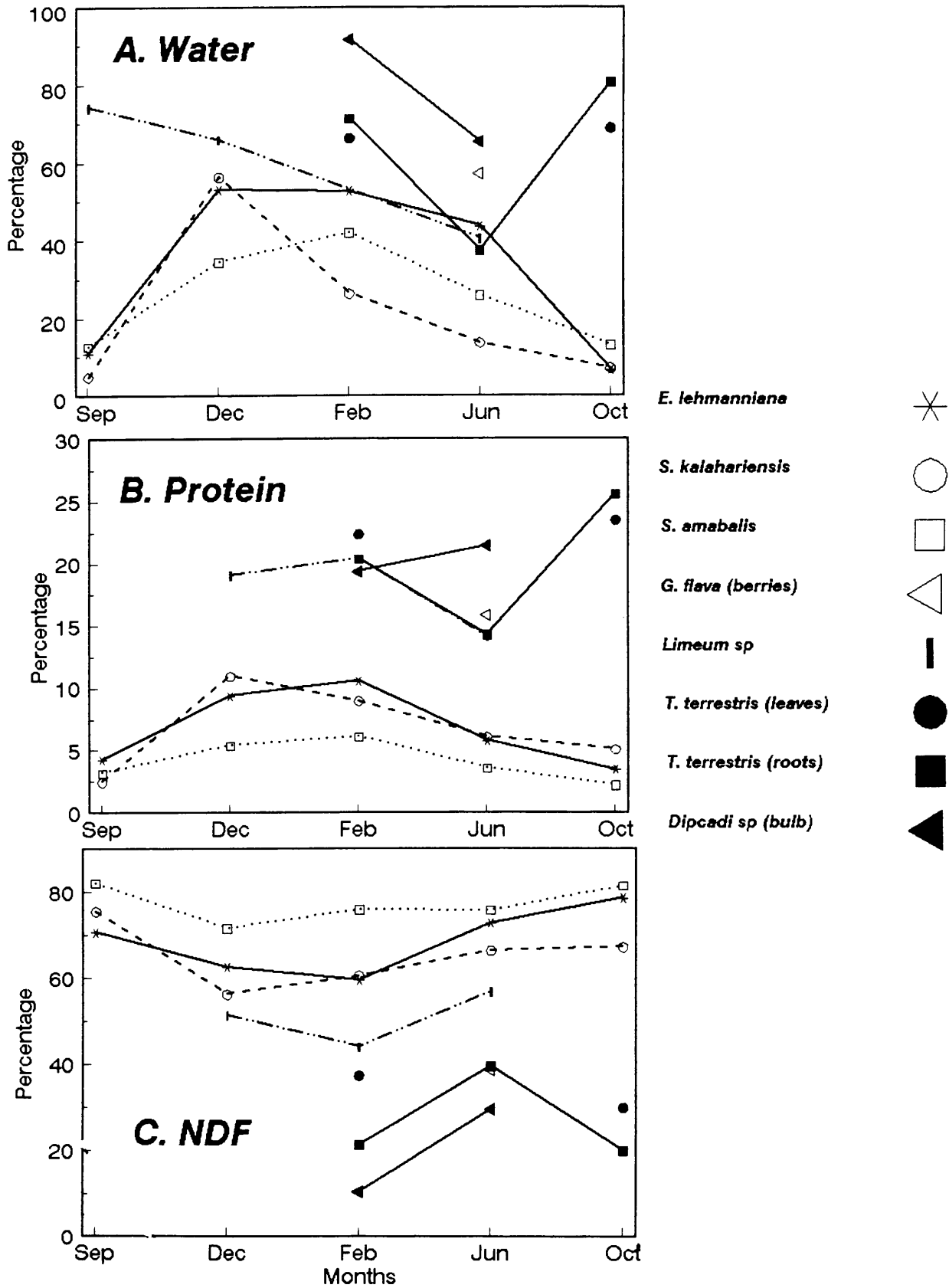
Fig. 2 The water (A), protein (B) and NDF (C) of preferred foods of X. inauri s.

Legend:
- E. lehmanniana — ✳
- S. kalahariensis — ○
- S. amabalis — □
- G. flava (berries) — ◁
- Limeum sp — |
- T. terrestris (leaves) — ●
- T. terrestris (roots) — ■
- Dipcadi sp (bulb) — ◀

Consequently the parts usually eaten were the most nutritious and softest parts available, high in energy and water content. Gross energy value of grass leaves were similar regardless of the seasonal patterns shown for protein and water. The average energy of the three grass species (Fig. 2A, B & C) was 15,8 ± 2,0 kJ/g dry mass. However, the digestibility of grass species probably varied seasonally as a result of senescence.

The bulbs of D. glaucum contained higher energetic values of 19,2 kJ/g dry mass. Similar values were found for G. flava berries of 20,05 ± 2,0 kJ/g dry mass. Usually X. inauris took the softest meristematic tissue at the base of grass blades, as well as fruits and flowers, and the drier leaves were discarded. In contrast to S. beldingii (Eshelman & Jenkins 1989), X. inauris would select a certain species and if this was abundantly available, concentrate on it to the exclusion of other species on its foraging path, occasionally taking some other plant part. Whilst the best quality food was taken whenever possible throughout the year, considerable quantities of fibre were also ingested and selected for at times. The stems of a grass species such as S. amabilis for example, were taken in conjunction with old Tsama runners during winter.

Table 5. A summary of the average plant water percentage and dry plant production/½yr at 'A. haem', exclusion plot, near the X. inauris study area.

Plant production	Feb 1987	Sept 1987	Mar 1988	Oct 1988
Average % H_2O in plants inside plot	58,38 ± 2,5	9,13 ± 5,6	54,04 ±5,0	22,49 ±3,2
average % H_2O in plants outside plot	57,51 ± 3,0	5,09 ±2,4	48,04 ±3,5	15,71 ±3,2
g yield /m²/½ inside plot	82,05 ±18,26	68,37 ±19,51	125,87 ±22,00	114,20 ±40,70
g yield/m ²/½y outside plot	60,55 ± 8,26	51,49 ±11,30	107,00 ±10,20	74,74 ±10,00
Student t-test: yield outside / inside plot	$t=1,80$; $df=18$; $P<0,05$	$t=1,91$; $df=18$; NS	$t=1,77$; $df=18$ $P<0,05$	$t=2,04$ $df=18$ $P<0,05$

These fibrous foods probably caused the passage rate of digesta to decline, but simultaneously, the microbiota of the large caecum had more time to ferment the cellulose (Chapter 6).

Table 5 summarizes the data collected at the 'A. haem' quadrant. The percentage water content of species inside the quads was slightly higher than those measured outside. During the summer months the outside vegetation contained an average of 48 - 57 % water and only 5 - 15 % water was available during late winter and early summer. The yield g/m² (air-dried weights) for 1987 was lower than that of 1988 and could be related to rainfall (Appendix 1). The effect of feeding by ungulates and rodents outside the A. haem quadrant, accounted for the significant lower outside values of yield (Table 5).

Notwithstanding the fact that the subterranean organic matter (Table 6) was found to contain significantly more water than the plant material above ground

Table 6. The available biomass of bulbs and roots (g /0,5m²) weighed from exclusion plots at the 'Rodent Hill' X. inauris study sight.

Plant production	Oct 1987	Dec 1987	Feb 1988	Jun 1988
Surface dry plant *yield g/0,25m²	27,6 ± 13,2	64,7 ± 20,3	85,8 ± 17,3	5,1 ± 2,6
Subterranean (20 cm) dry plant yield g/0,5m²	46,2 ± 15,7	92,0 ± 31,2	79,7 ± 8,9	33,2 ± 8,1
% water surface yield	40,2	60,4	62,0	25,0
% water root/bulb yield	46,2	77,5	80,0	61,8

* Yield = dry biomass

($t = 1,65$; $df = 36$; $P < 0,05$), the dry mass of food available underground was not significantly higher than above ground ($t = 0,74$; $df = 36$). Consequently X. inauris have a water source available in the form of underground roots and bulbs throughout the year, but the plants above ground were eaten whenever these were still green and succulent. More digging occurred during the the cold-dry winter months when the biomass above ground was close to zero and a

substantial amount of bulb material was available underground (Chapter 4). However it would be more advantageous to feed above ground as it is energetically less expensive and permits constant vigilance. Digging for a food item also took more time and energy, than above ground picking of leaves or flowers.

Feeding, itself entailed smelling along the surface until a morsel was discovered. Each kind of food was collected and eaten in a similar fashion. Large leaves, flowers, roots and berries were bitten off with the incisors at the base and transferred to the forepaws and eaten while sitting up. The softest most nourishing pieces of a blade or stem was then bitten off and chewed, while the rest was discarded, all in a rapid performance. The seeds of berries were also consumed and could be traced in the faeces. Roots and tubers were obtained by digging holes of as deep as $20,0 \pm 5,0$ cm (N=22), and could envelop the squirrel's whole body. Foraging behaviour, digging and climbing will be discussed as an integral part of all other activities in Chapter 4.

Although the foods eaten were extremely diverse, the important items in the diet tended to be nutritionally superior. Predominant plant foods were green grass blades, starch-filled roots, which were high in carbohydrates and water, and berries, which were high in protein (Fig. 2). This pattern of preferential feeding on high-quality foods has been reported for several other rodent species (Clark 1981, Karasov 1985, Eschelman & Jenkins 1989).

B. BURROWS

Many rodents, because of their size and thermal sensitivity, have made maximum use of nests and burrows, extending their range into another habitat dimension to avoid exposure to macro-climatic extremes. This has allowed them to extend their distribution to several habitats where other mammals find living

extremely difficult (Hart 1971). Studies on social organization often include the distances between burrows, their position and importance (Karasov 1981, Kuhnen 1986, Ferron & Quellet 1989, Kawamichi 1989). A general knowledge of the use of micro-climates by small mammals is essential for the interpretation of the relationship between physiological functions, such as metabolic rate and water metabolism and the environmental temperatures that these animals are exposed to. However, it is possible that burrowing, as a pre-adaptive feature, has its significance not in thermoregulation, but in reducing mortality from predation (Armitage 1981). It therefore follows, that the understanding of an animal's physiology must also involve precise and detailed information about its behaviour. The subterranean burrows and runways that are potential resting places for X. inauris were numerous in all areas where they were resident. It was of primary interest to compare prevailing microhabitat temperatures as well as the structure of X. inauris burrows.

Methods

Burrows were identified in the behaviour study area and charted (Fig. 1B). Five burrow systems were excavated in the dune veld near Nossob camp and the results are summarised in Table 7. The average width, length and location of nest position were measured at six random places in the excavated burrow system.

Table 7. Five excavated dune burrow systems of X. inauris. Width = w (mm); depth = d (mm). A = Acacia; P = periphery; C = central.

Nest position	Nest location	Nest w	Nest d	Nest material mass (g)	Tunnel w	Tunnel d	Number exits
1 A. mellifera	C	260	700	600	124 $\pm$ 17	620 $\pm$ 84	8
2 A. mellifera	P	260	600	500	132 $\pm$ 23	680 $\pm$ 130	8
3 Rhigozum	P	270	700	650	148 $\pm$ 11	700 $\pm$ 71	9
4 Open	P	240	750	600	140 $\pm$ 26	720 $\pm$ 164	7
5 A. mellifera	P	280	800	750	140 $\pm$ 14	640 $\pm$ 134	9

Environmental soil and burrow temperatures (at various depths) were recorded with an MCS 101 computing data logger fitted with thermistor probes. Temperatures were recorded twice during the hottest and coolest months in KGNP, January and July of 1987 and 1988 respectively. The data logger was programmed to record instantaneous temperatures at 30 min intervals for four consecutive days. Ambient temperatures were recorded at 1) 1 m above ground in the shade 2) at ground level 3) 40 and 80 cm within burrow tunnels, while black-bulb temperature was measured 1m above ground in the open. Soil and ambient maximum and minimum temperatures were also recorded during the behavioural study throughout all seasons of one year.

Results and discussion

Over 44 of the 53 burrows in the study area were frequently used by both adult males and females (Fig 1B). Up to 80,0 % of the burrows in the behaviour study area were constructed in well-shaded habitats under bushes, at the bases of large trees, inside old tree-trunks or in termite mounds. Three reasons could be given for this. First, shaded environments provided cool constant burrow temperatures which were important in this semi-arid environment. Kenagy (1973) also found that Dipodomys microps, Dipodomys merriami and Perognathus longimembris constructed burrows under thick vegetation as a means of ensuring cool burrow temperatures. Secondly, the shaded areas around the burrows probably provided protection for X. inauris from predation, especially raptors. Similarly, shaded vegetation was used for burrows by giant rats (Cricetomys gambianus) (Knight 1983). Thirdly, construction under vegetation and in harder substrates, such as termite mounds lends support to tunnels and prevents caving in, since tunnels and chambers are large in size and the red sands are usually very loose, lacking the binding power of roots.

Not only do they use them to escape the extremes of the external macroclimate and predators, but they are also used for resting during day and night
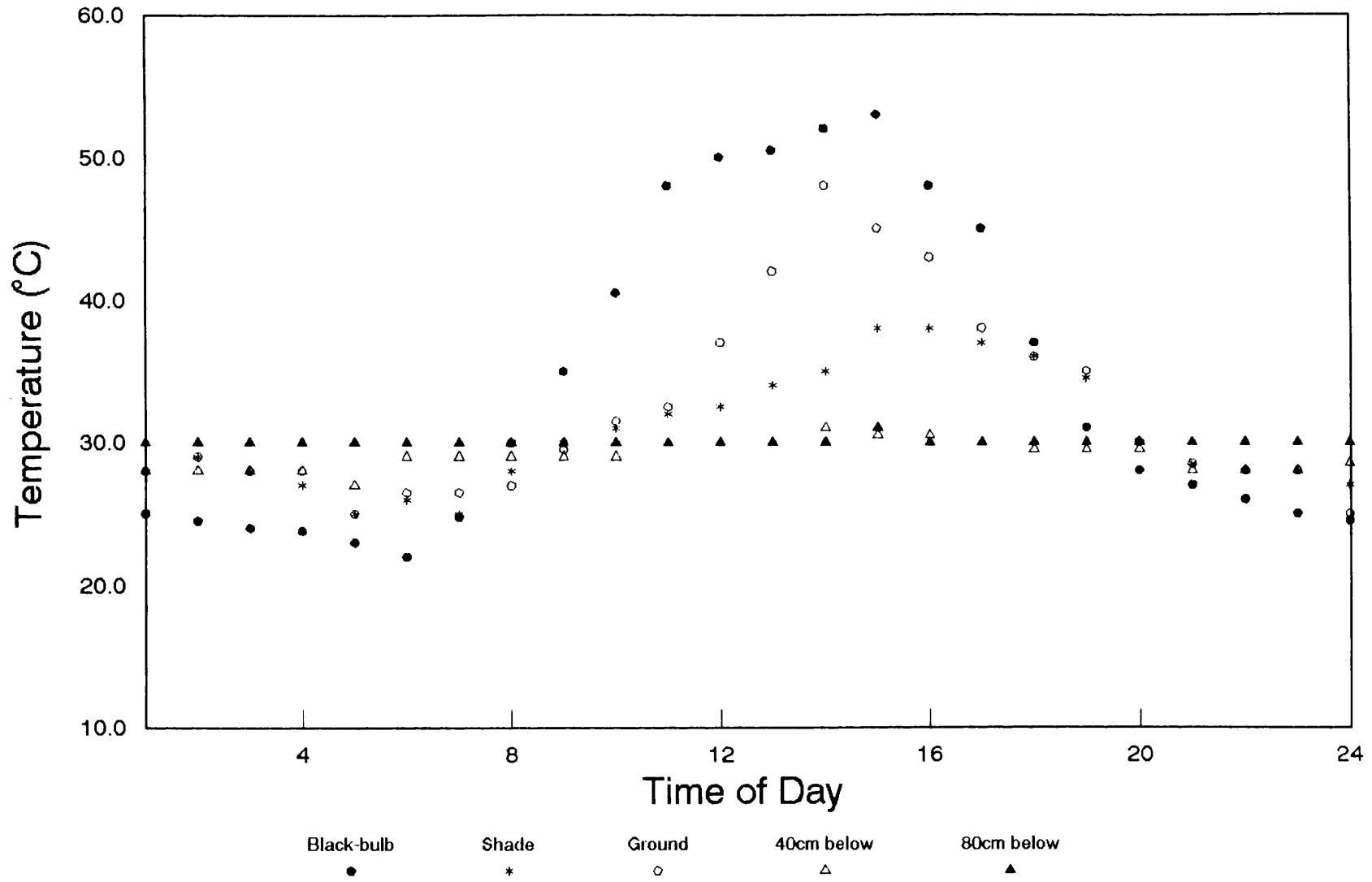
Fig. 3. The summer ambient temperatures measured above and within the burrows of X. inauris.
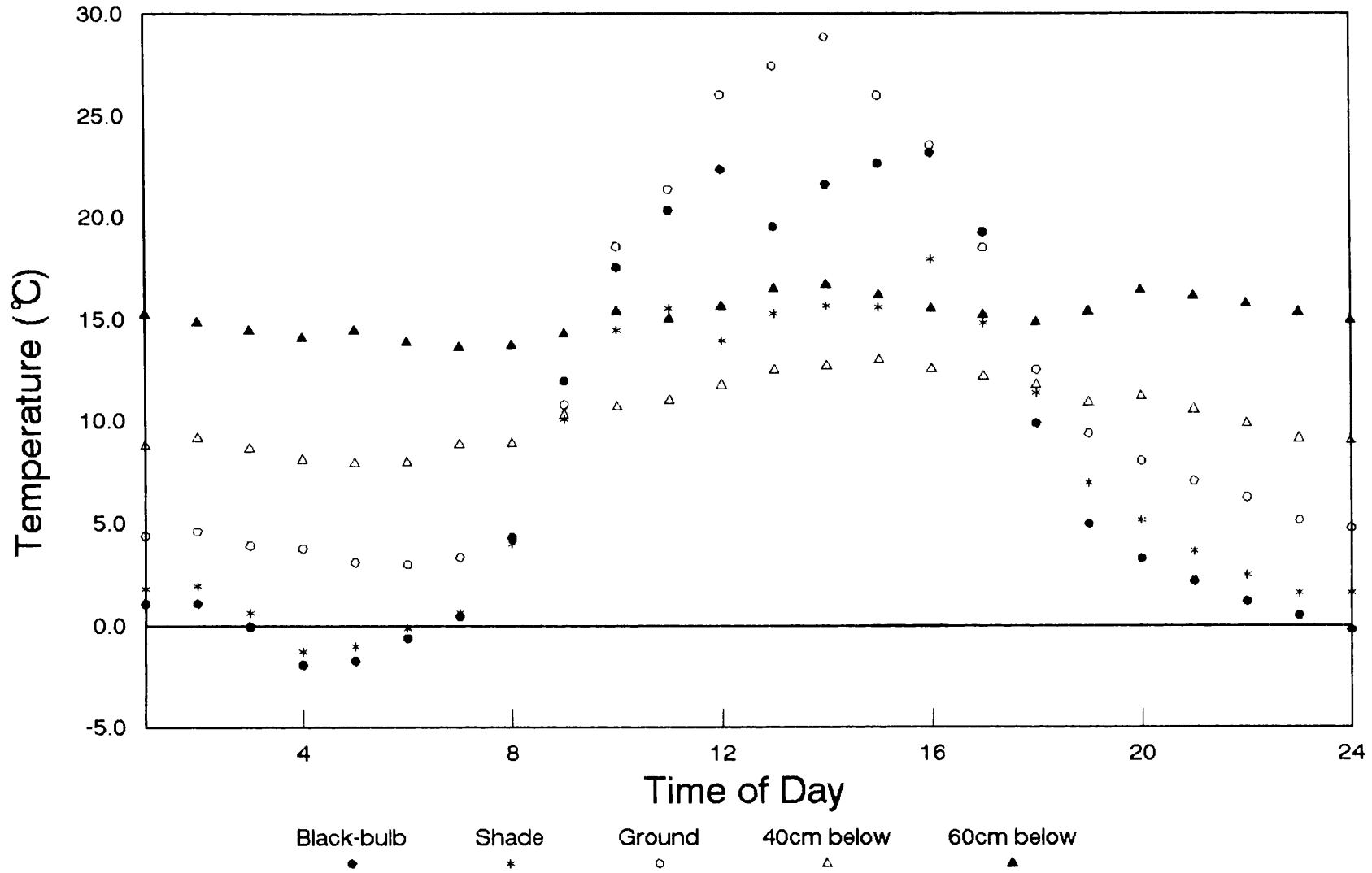
Fig. 4. The winter ambient temperatures measured above and within the burrows of X. inauris.

and for rearing their young. No plugged holes were found in the burrow sytems of X. inauris and no defaectaria were located. X. inauris defaecated while foraging. No coprophagy was observed in captivity or in the wild. The most used burrow entrances had a dome-shaped mound, while the least used burrows lacked soil around the entrances and were usually used as escape refuges. Large scale digging of complete burrow systems by squirrels was never observed. They rarely cleaned out entire burrow systems, however burrow entrances were cleared and squirrels tended to rather take over or share old suricate (Suricata suricatta) burrows. They were also found to extend the vacated burrow systems of whistling rats (Parotomys brantsi).

The contents of nesting chambers usually consisted only of grass and no hoarded food. During the early summer pregnant females collected pieces of grass leaves, which they carried in their mouths to the central burrow system. Burrow systems formed a complex network of interlacing tunnels. No plugged entrances were found. Burrow systems covered areas of between 45 m^2 and 130 m^2. Eighty percent of the nesting chambers were situated on the periphery of the burrow system. Average nest width was 262 $\pm$ 15 mm which was significantly wider than that of the tunnels 136 $\pm$ 19 mm (t=-13,78; df=28,0; P<0,001). The depth of the nests and tunnels did not differ significantly and measured 710 $\pm$ 74 mm and 672 $\pm$ 117 mm respectively. X. inauris nesting chamber sizes were comparable with the chamber sizes of Eutamias sibirians 244 x 246 mm (Kawamichi 1981) and E. amoenus 152 x 171 mm (Broadbrooks 1958). The mean weight of nesting material in X. inauris nesting chambers, mainly grass blades, was 62,0 $\pm$ 9,1 g (n=6). Having numerous entrances to the burrow system is an advantage for rapid escape from predators, particularly when living in groups. Furthermore, several entrances would be important as escape routes against ground predators such as snakes entering a burrow system. The large entrance widths facilitate air circulation as witnessed in the normal oxygen and carbon dioxide levels, as measured in several squirrel burrows in the Kalahari Gemsbok National Park (Buffenstein, pers comm.). The

wide tunnels (squirrels could turn inside them) were also advantageous as CO_2 build-up was prevented.

The effectivity of the burrow systems in providing shelter from climatic extremes can be deducted from Figures 3 and 4. Mean daily maximum temperatures of the burrow at 40 and 80 cm during summer were at 29,9 $\pm$ 1,5° C and 30,6 $\pm$ 0,1° C respectively and never exceeded 31,3° C. These daily average maximum burrow temperatures fell within X. inauris TNZ, measured under resting metabolic circumstances by Haim et al 1987. Mean daily burrow winter temperatures were less constant and varied between 10,3 $\pm$ 1,7° C at 40 cm and 15,1 $\pm$ 0,9° C at 80 cm. Lowest temperatures in the burrows during winter never declined below 7,0° C (Fig. 3). During summer mornings and siestas, squirrels would emerge from different burrow exits of the central burrow system but the reverse was true for winter. Group members would emerge from one entrance, usually centrally located. Long sessions of huddling and grooming of up to 80,0 $\pm$ 5,0 min at the entrance of burrow systems occurred during winter mornings and late afternoons, with shorter periods (20,0 $\pm$ 4,0 min) during summer mornings (Chapter 4).

Shape, size, complexity and depth influence burrow environments, as does soil type. Hooper & El Hilali (1972), Kay & Whitford (1978), Karasov (1981), Kuhnen (1986) and Kawamichi (1989) discussed thermal gradients, moisture and CO_2 concentrations as well as nest dynamics of rodent burrows. The vertical thermal gradient within burrow systems gives the opportunity of selecting a location in a burrow at which the least energy is necessary to regulate body temperature. Kenagy (1973) reported intra-burrow temperature selection movements of D. microps and D. merriami. The moderate and stable thermal fluctuations within rodent burrows follows the above surface temperature (Baudinette 1972). The burrow temperature is the equilibrium value of burrow air and the surrounding soil (Hayward 1965). The central burrow system of X. inauris was used overnight by all group members and for siesta rests (Chapter 4). All other burrows in the home area were used on an ad hoc basis for refuge

from predators and the extreme temperatures in summer. Any environmental temperatures outside the thermal neutral zone of between 29 and 33° C (Haim et al. 1987) would place demands on the squirrels' metabolism (Chapter 5). It would therefore be advantageous to rest in a burrow system within a stable temperature regime during extreme ambient temperatures.

C. REPRODUCTION

As in most sciurids, the male-female pair bond was not a fundamental unit in the social life of X. inauris. Males did not take care or provide for the young. Michener (1983) described most sciurids such as Richardson's ground squirrel Spermophilus richardsonii as being polygynous and no permanent pair bonding beyond copulation occurred. In this species however, the female-infant bond and the mothers and daughters specifically interacted amicably, having coinciding ranges (Chapter 4). The gestation period was between 42 and 49 days, which was longer than the average for squirrels in general. Apart from the oldest female, the other adult female in the group also produced young, usually having at least one litter of twins a year. Females from the same group were seen to share the rearing of young and allo-suckling was observed on many occasions.

In X. inauris the altricial young open their eyes when 35 days old and appear above ground 40 days after birth (Smithers 1983). In the Kalahari, breeding has been noted to be seasonally restricted occurring once each summer season. Females came into oestrus during October, when mating occurred. However, during higher than above average rainfall years (>220 mm), females can have two litters per season and rear up to four young per litter as happened with one female on two occasions during the summer season of 1988/1989. Females start foraging about four days after giving birth, returning frequently to the burrow, presumably to suckle their young. The number of pups per litter ranged from

1 to 4 with a mean of 2 $\pm$ 1,5, with the sex ratios of juveniles being 1:1 (N = 18).

Growth and development continued until the age of five months and was similar to that described in detail by Herzig-Straschil (1978). The exact lifespan is unknown but one individual was recorded as surviving for a minimum of five years.

D. RELATIONS WITH OTHER ANIMALS

Ground squirrels often share a burrow system with yellow mongooses Cynictis pencillata and suricates (S. suricatta). Moreover, other animals such as the blue headed agama (Agama hispida) and the barking gecko (Ptenopus garrulus) lived in the burrow entrances of squirrel burrow systems. Several insects (Coleopterans) and scorpions (Scorpionidae) dug their burrows in the entrances of burrows. Ground squirrels are always acutely alert even when relaxing, their eyes being situated on the sides of their heads giving them vision in all directions (360 °) (Chapter 4). However, they did depend, apart from their own group members, on other animals to warn them of predators. The raucous call of the black korhaan (Eupodotis afra afra), the sudden whistle from the whistling rats (P. brantsi), and the barking of suricates, all functioned as alarm calls. Large raptors such as the martial eagle Polemaetus bellicosus and the chanting goshawk (Melierax musicus) were observed to attack squirrels, while De Graaff (1981) reported that owls such as the giant eagle owl (Bulbo lacteus) take ground squirrels. This possibility cannot be excluded in the Kalahari as owls started their hunts during twilight when squirrels were sometimes still outside their burrows. Jackals (Canis mesomelas) and Cape foxes (Vulpes chama) were also avoided. Several encounters with Cape cobras (Naja nivea)(and puff-adders (Bitis arietans) have been observed. As soon as a snake was spotted, squirrels would mob it and drive it away from their burrows (Chapter 4).

Fleas of three different families associate with <u>X. inauris</u> and therefore these squirrels have been described as vectors of several diseases. They harbour ticks that transmit biliary fever, East Coast fever and tick-bite fever (Theiler 1962).

<u>Summary</u>

Food plants such as <u>E. lehmaniana</u> and <u>T. terrestris</u> provided succulent leaves, stems, flowers and roots throughout the year. Such plant material served as a water and protein source for <u>X. inauris</u> during the hot dry summer when the nutritional contents of preferred food items tend to decline. Although the plantparts taken were diverse and ranged from flowers, leaf blades and stems to berries, a combination of succulence and availability ensured a pattern of high-quality feeding material throughout the year. The central burrow was used overnight and during siestas by all group members and these sytems have enough space to ensure no build-up of CO_2. Furthermore, it is advantageous to escape the macro-climatic extremes as well as predators in a very convenient and available micro-climate. <u>X. inauris</u> share their burrows with other species such as yellow mongooses and suricates.

CHAPTER 4

BEHAVIOUR OF FREE-RANGING SQUIRRELS

INTRODUCTION

In semi-desert environments resources are limited and studying adaptations that have evolved in response to extremes are challenging. Not only does homeostasis with all its advantages cause some substantial physiological burdens that have to be tolerated but also remarkable functional behavioural changes (Dawson, Pinshow, Bartholomew, Seely, Shkolnik, Shoemaker & Teeri 1989).

X. inauris, is a diurnal, colonial and relatively large rodent. The open vegetated habitat in which these squirrels live is an ideal area for studying behaviour and ecological interactions. Furthermore, being a highly successful herbivore, which lives in burrows as cohesive colonies or coteries (Bowling 1958, Straschil 1975) probably caused the typical behavioural escape the midday heat and/ or usage of a parasol tail for protection and water conservation. Apart from the unpredictable physical environment surrounding them, X. inauris must also be capable of escaping from enemies and defending themselves against other squirrels, as well as feeding efficiently. The quality and quantity of foodstuffs available and how these could be utilized also affect animal behaviour (McGinley & Whitham 1985, Andrusiak & Harestad 1989, Bergeron, Brunet & Jodoin 1990). Consequently it can be expected that a conflict exists between maximizing nutritional and reproductive objectives and minimizing exposure to predators and the weather.

Apart from Herzig-Straschil's (1978, 1979) and Smithers' (1971) studies on the natural history of X. inauris, very little is known about their behaviour. It was hypothesised as a motivation for the study in general that, because of their relatively large size and colonial habits, X. inauris is able to survive in a semi-

desert area (Chapter 1). A study of a group of squirrels in the red dunes of the southern Kalahari was conducted over a period of approximately one year and observations on their activities, use of space and some social aspects of their behaviour in relation to environmental and seasonal variables were made. The following questions were asked:

1. What role does season and temperature play in daily activities ?
2. What role does sociality play during daily activities ?
3. What role does predator avoidance play?
4. How do squirrels use their home range?

METHODS

Temporal patterning of activity

Activities of a group of five squirrels living in the red dunes, three km west of Nossob camp were observed for 320 h (39 days) between August 1987 and June 1988. All observations were made using 7 x 35 binoculars from a parked vehicle 10 to 30 m from the group.

Data were collected using the instantaneous scan sampling method (Altmann 1974) as described by Lehner (1979) with a five min interval between records of activities of all individuals. Animals were individually recognised from markings and scar patterns. When the group size and/or foraging range became too large to allow accurate sampling per 5 min, the sample interval was changed to 10 min. A bout was defined as a period of activity occurring repetitively or as a change from underground to surface activity. These bouts were separated mainly by the midday siesta. Surface activity bouts were 3h 36 min ± 10 min long. The time spent above ground in locomotion and feeding is given in Table 9.

Although the sampling method gave a clear general view of time allocated to different behaviour patterns, and some seasonal trends, males and females did not differ in activity patterns, data were lumped for further analyses (T-test). The behavioural categories recognised were mutually exclusive (McFarland & Sibly 1975). They were as follows:

1. Standing

The animal is stationary on all four feet. The feet are placed apart from each other. Several quadrupedal postures occurred during activity patterns and could could be defined as follows:

a. Stand vigilant (on all four feet in a vigilant position); b. stand feed (on all four feet in a feeding position); c. stand-up vigilant (on two feet); d. auto-grooming (on all four feet); c. allo-grooming (on all four feet); d. anal-sniffing (on all four feet); e. nasal sniffing (on all four feet); f. mounting (on two feet); g. suckling (on all four feet); h. defaecating (on all four feet).

2. Sitting

Describes stationary animals either sitting on their hindfeet without the fore-paws on the ground (squatting) or sitting-up (look-out posture) on their hind feet, with the forepaws off the ground. The following behaviour patterns could be identified while squirrels were in the sitting position:

a. Sit on hind-feet vigilant; b. sit-up on hind feet feeding; c. sit-down on hind feet feeding.

3. Walking

Walking describes movement with the four legs of the squirrel and all four feet diagonally placed in sequence. The following behavioural patterns could be identified while walking :

a. Walk (head down); b. walk (head bob); c. crawl (head down); d. crawl (head bob).

4. Running

The animal moves rapidly using a trotting gait, sometimes galloping or jumping. While running the forefeet are placed alternately, but the hindfeet are placed on the ground more or less in unison. Running could be observed during the following activity patterns:

a. Run (head down); b. fight; c. play;

5. Digging

Digging could be classified as being done at different depths in relation to the amount of body exposed above the surface. The animals dig, using their paws in a synchronised fashion. They sniff the surface and then proceed to dig with their forepaw claws, scratching and excavating or turning over the soil and pushing the soil away into a little mound. The following activity patterns were observed while digging.

a. Dig up to shoulder height; b. dig until half the body dissappears; c. dig until the whole body was underground;

6. Climbing

Animals reach up with their forepaws while standing on the hindlegs. They then climb slowly with the diagonal leg movement sequence used during walking. The tail is used in balancing and is of considerable assistance, in climbing down when it is pressed onto the substrate to exert a braking action. Sometimes animals clinging onto a branch of a G. flava bush lost their balance, let go and fell onto the sand below. Feeding took place intermittenly while climbing.

7. Lying

The animal lies on its belly in a crouched prostrate position with the tail down. Lying on the side or back occurs on occasion. The following behavioural activities could be listed:

a. Prostrate resting; b. back lying; c. basking; d. sandbathing.

Tail orientation, vocalization and position to closest burrow and individual were noted with each behaviour (Golightly & Ohmart 1978, Viljoen 1980, Karasov 1985, Lima 1985).

Climatic variables were noted every half-an-hour, or when changes occurred, and included : cloud cover (0-5 scale); wind speed (measured in m/sec with a Wind Wizard speed indicator; Davis instruments; Leandro, USA); ambient temperature and soil temperature. Behavioural patterns were divided into four main categories (vigilance, feeding, resting and socializing) and compared per season to evaluate the influence of climate on activites and whether any seasonal differences were apparrent.

The vegetation of the study area was assessed throughout the study period. Variation in plant species, cover and underground availability of bulbs and other roots were monitored. The preferred plant species are listed and discussed (Chapter 3).

Group sizes were monitored during regular road counts made on 490 km of dirt road within the Kalahari Gemsbok National Park over a five year period, from 1985 until 1989. This data are discussed in Chapter 5.

Burrows from which animals emerged in the morning were presumed occupied by squirrels as overnight shelters. Each burrow site was recorded precisely in the field and later marked on a detailed map of the study site (Chapter 3).

Spatial relationships

Whenever any behaviour pattern was recorded the distances between individuals, their distance from the closest burrow and group foraging width were estimated and noted.

Seasonal home ranges for individuals and age/sex groups were calculated by the convex polygon or minimum area method (MAM) (Mohr 1947) using the MCPAAL program written by students of the National Zoological Park, Smithsonian Institute, 1985. An animal's home range is usually defined as that area covered in normal daily activities (Lehner 1979). The non-parametric core convex polygon method by Kenward (1987) was used to show the area used and the intensity of the area used as a percentage of ha and drawn in graph format.

All frequency data were arcsine transformed before being tested for differences. Differences and analysis of variance were tested using ANOVA tests (SAS 1988). All data were converted to rates of total time observed per individual. The Chi-square (X^2) and Mann-Whitney U test were used as non-parametric data sets or frequency data tests (Siegel 1956). Correlations were determined using Pearson's correlation in the SAS programme (SAS 1988).

RESULTS

Demography.

The squirrel group under observation consisted of five members when the study commenced in August 1987: two adult females, one about three years and the other about two years of age, a sub-adult male, aged about six months and two juveniles, a male and a female, about two months old until December 1988, when they disappeared. During that month the group consisted of only three members, but the oldest female was in an advanced state of pregnancy giving birth in early January twins, a male and female, which emerged above ground at the end of January. Two adult bachelor males, both about three years old, visited the females on an irregular basis throughout the study, but neither became resident. By the beginning of March the juvenile sub-adult male had disappeared. The sub-adult resident male had disappeared by the end of March

1988 and group size again totalled three. However two litters were born, one to each female at the beginning of April 1988. The older female had three pups, two females and a male, the younger female a male and female. The total number in April 1988 was eight. The male pup in the litter of three disappeared in May 1988, a week after the young of both litters emerged above ground. When the study ended in June 1988, the group consisted of seven squirrels (Table 8).

From the average group sizes measured over a five year period in the Park (KGNP) (Chapter 5), it became apparent that coteries averaged 4,0 $\pm$ 1,2 individuals and that coteries overlap rather than being territorial.

Temporal

Above ground activity

The general activity on the surface was synchronised and when one member of the group emerged, the others soon followed. The time interval between the first and last squirrel to emerge was 15 $\pm$ 5 min. Similarly, members would take a siesta simultaneously, with the time lapse between first and last individual going down the burrow being 10 $\pm$ 4 min (n= 35) when the ambient temperature rose above their thermoneutral zone (Fig. 6 A, B & C).

Two bachelors occasionally visited the female group. However the data in Table 9 give an average indication of lumped daily activity of all group members and includes when activity commenced and terminated. Rates of activity, taking the number of individuals per sex and class, hours of observation and numbers of observation in consideration, was used to determine the differences between classes of squirrels.
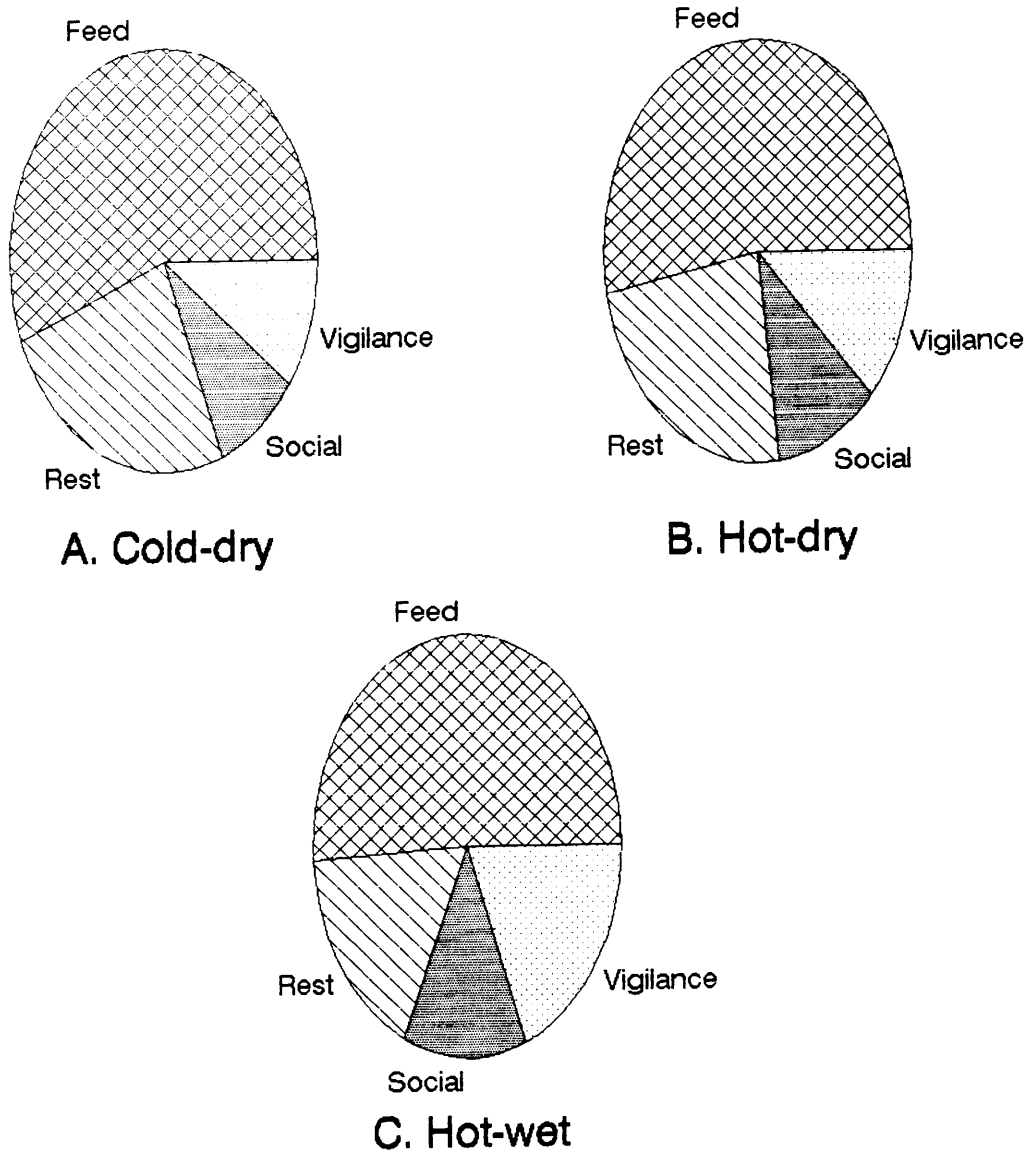
Fig. 5. Seasonal diurnal activities of X. inauris.

Table 8. Demographic characteristics of the X. inauris group studied at 'Rodent Hill' near Nossob from August 1987 until June 1988.

AGE-CLASS		MONTHS				
1987		AUG	SEP	OCT	NOV	DEC
ADULT	♀	2	2	2	2	2
	* ♂	2	2	2	2	2
SUB-ADULT	♀	-	-	-	-	-
	♂	1	1	1	1	1
YOUNG	♀	1	1	1	1	-
	♂	1	1	1	1	-
TOTAL GROUP SIZE		7	7	7	7	5
1988		JAN	FEB	MAR	APR	JUNE
ADULT	♀	2	2	2	2	2
	* ♂	2	2	2	2	2
SUB-ADULT	♀				1	1
	♂	1	1			
YOUNG	♀	1	1	1	3	2
	♂	1	1		2	2
TOTAL GROUP SIZE		7	7	5	10	9

* Adult males were non-resident but visited the group occasionally.

The squirrels typically spent 6 - 7 h per day on the surface (Table 9). No seasonal trend was found, but this could be due to the limited number of observational days for each season (Table 9). However the biphasic activity pattern, which included siesta-periods, was significantly different between seasons ($X^2 = 19,88$; df=4; P= 0,012) (Table 9). The siesta periods during winter were short and increased in length during summer. The high ambient temperature recorded for the mid-day period probably accounted for this difference and is illustrated in Figure 6A, B & C. Squirrels averaged 2,5 ± 0,5 bouts of activity on the surface per day.
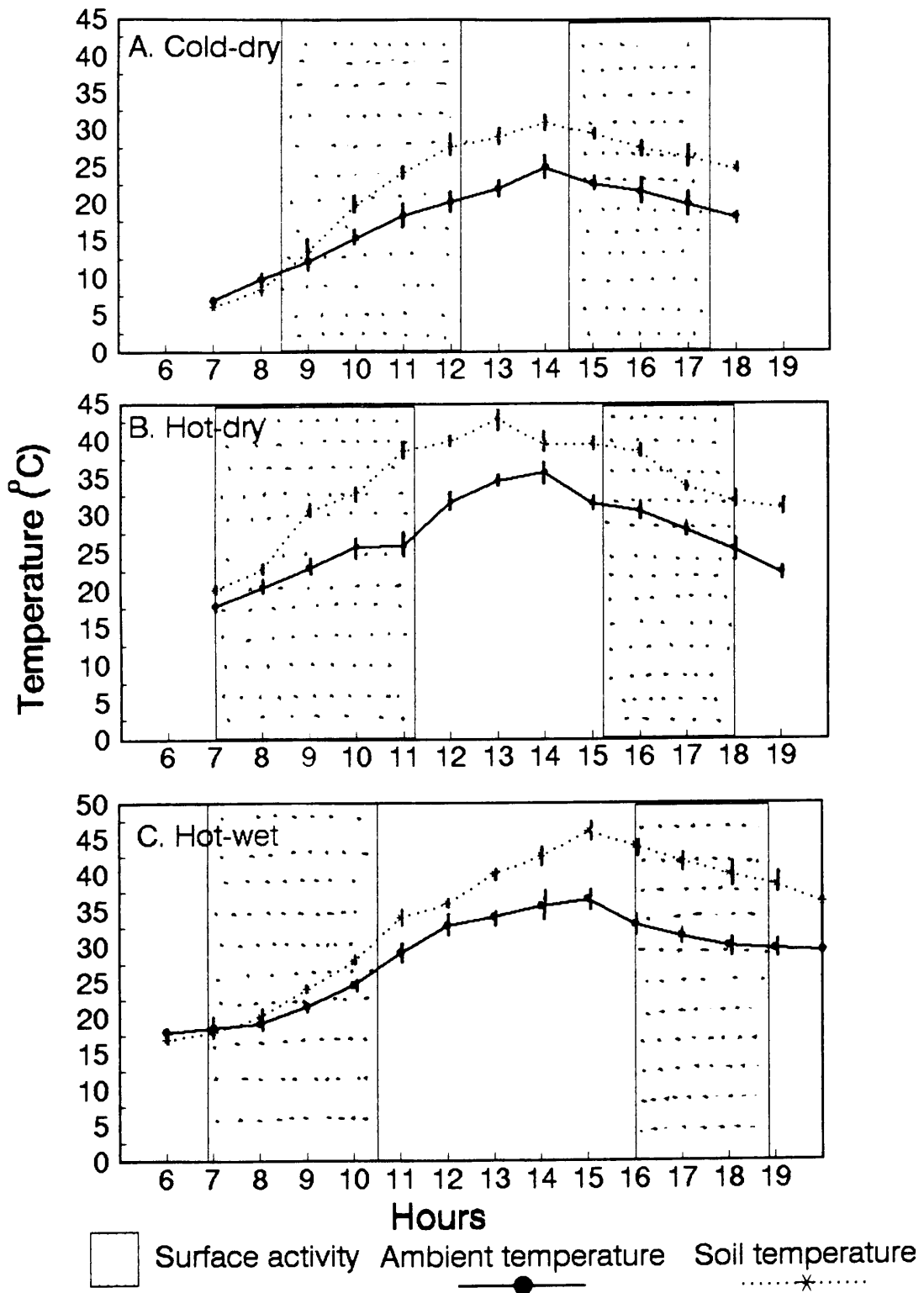
Fig. 6. Time of above ground activity of X. inaurus against ambient and soil temperature.

Table 9. Above-ground activity of a group of X. inauris over a period of
a year. CD= cold-dry season; HD= hot-dry season; HW= hot-wet
season. N= total days of observation.

| | SEASONS | | |
	CD	HD	HW
Total time and days of observation	129 h n=10	93 h n=14	98 h n=15
Onset of activity (hours after sunrise)	2,15 ± 1,0	1,15 ± 0,5	2,00 ± 0,5
End of activity (hours before sunset)	0,67 ± 0,05	0,20 ± 0,05	0,40 ± 0,05
Total time (min) above ground	391±25	367±20	387±28
Number of above-ground bouts/day	2,0 ± 0,5	2,8 ± 1,0	2,5 ± 0,5
Time spent as siesta (min)	269±30	303±20	353±40
Duration of above-ground bouts (min)	216±12	203±10	210±18

Climate

The ambient and soil surface temperatures while squirrels were active above
ground showed significant differences between seasons ($X^2=326$; df=28;
P=0,0001). The mean ambient temperature at 08h00 in the morning was
$24,5±2,4$ °C in the hot-wet season. Soil surface temperatures followed the same
pattern at much higher levels and measured as high as $46,0±3,9$ ° C when
squirrels emerged to forage in short spurts during the mid-afternoon on hot
summer days (Table 10) (Fig. 6 A, B, & C).

Resting and social behaviour showed significant differences during the cold-dry season when tested against the ambient and soil temperatures (Fig. 5; Table 10). Only resting was influenced by ambient temperature during the hot-dry season and activities were independent of ambient temperatures during the hot-wet season. Resting was inversely associated with soil temperatures during the cold-dry and hot-wet seasons, while socializing was significantly influenced by soil surface temperature only during the cold dry season. None of the activity parameters were significantly influenced by soil temperature during the hot-wet season (Table 10).

Wind and general activity were significantly correlated ($r = -0,5566$; $N = 60$; $P = 0,0001$) for all seasons. Whenever the windspeed was faster than 10m/s, squirrels curtailed their activities temporarily, only making short visits above the surface. On days when sandstorms prevailed, raising the dust so that visibility was limited to 1,0 m (windspeed = 15-18m/s), squirrels did not emerge at all.

Feeding activities were substantially depressed but not absent on the few rainy days squirrels were observed.

Apart from using the shade of their burrows, above-ground shade-use was apparent. Shade use differed significantly between seasons being highest during the hot-dry season ($F = 5,89$; $df = 2\&1$; $P = 0,0037$) (12,3 %) and lowest during the cold-dry season, (6,9 %) the hot-wet season being intermediate (7,9 %).

Table 10. The analysis of variance between X. inauris activities versus ambient and soil temperatures were tested by season. (CD = cold-dry season; HD = hot-dry season; HW = hot-wet season, P < 0,05)

ACTIVITY	AMBIENT TEMPERATURE °C		
	CD	HD	HW
FEEDING	NS	NS	NS
VIGILANCE	NS	NS	NS
RESTING	F = 10,61; df = 1; P = 0,0099	F = 12,59; df = 1; P = 0,0094	NS
SOCIALIZING	F = 8,70; df = 1; P = 0,0162	NS	NS
	SOIL TEMPERATURE °C		
FEEDING	NS	NS	NS
VIGILANCE	NS	NS	NS
RESTING	F = 13,91; df = 1; P = 0,0050	F = 17,99; df = 1; P = 0,0003	NS
SOCIALIZING	F = 7,79; df = 1; P = 0,0211	NS	NS

General activities

The surface activities of squirrels could be divided into four main categories: vigilance, feeding, resting and socializing. There were no significant inter-individual differences in the frequencies with which squirrels engaged in the four main activities (Table 11).

Vigilance

X. inauris appears to be continually alert in all postures or gaits and, as a result of their lateral and rather protruding eye position, they can look behind them without turning their heads. The three distinct vigilant stances were used to show concentrated or overt vigilance: 1. standing on the hind-feet with the body held erect, tail flicking, emitting a monotonous tone; 2. standing position on all

four paws, flicking the tail and vocalizing at times; 3. sitting on the haunches, vigilant looking around, flicking the tail and vocalizing. Raptors such as chanting goshawks (M. musicus) and bateleurs (Terathopius ecaudatus) were frequently sighted in the study area and elicited overt vigilant reactions whenever detected (Chapter 3). Furthermore, the presence of raptors in the study area could be positively correlated with rainfall (r= 0.49; P<0,05; n=42).

Overt vigilance made up between 8,5 and 13,7 % (mean 11,60 %) (Table 11) of the daily activities but did not differ significantly between seasons (X^2=0,844; df=4; P=0,932). However a trend towards more vigilant behaviour was noted from the cold-dry season through to the hot-wet season (Fig 5). All group members were found to be equally vigilant irrespective of age or sex (X^2=2,104; df=12; P=0,442).

Vocalizations and visual signals such as the flicking of the tail, or fanning out tail hair, holding the tail in an erect fashion, were used to alert fellow group members. A predator or enemy will be spotted well in advance of any disturbance and a flight distance between predator and prey of 65 ± 5 m (N=24) (or less) was kept. Vocalizations were overwhelmingly correlated with fighting and overt vigilant posture, making up 32 and 28 % respectively of all times when squirrels vocalized. Three distinct vocalizations were recorded: An alarm call, a high pitched sound which was usually overtly alert in a look-out position; a 'squeal-scream', produced when an animal is running away in great fear; and a snarl, a deep short sound heard in agonistic encounters. Predators such as jackals would approach squirrels as close as 5,0 m before residents would disappear into a burrow.

Tail flicking was not only associated with vigilance, but also with playing and fighting. Although tail flicking increased from 5,21 % during the cold-dry season to 7,63 % in the hot-wet season, these differences were not significant (X^2=9,955; df=10; P=0,444).

Head-bobbing occurred while <u>X. inauris</u> walked or crawled. It appeared to be a subtle initial signal of danger, e.g. predators nearing other members of the group or when a strange squirrel approached . It may also function as a flight precursor, i.e. the squirrels are ready to flee at any moment. It took up 2,0 % of the total activity time and a third of total walking and crawling time and appeared to occur equally frequently throughout the year (X^2 = 2,331; df = 10; P = 0,998).

<u>X. inauris</u> seemed to be little perturbed by snakes entering their home area. The squirrel tail played an important role during snake encounters and was bent sideways away from the body, and moved from side to side and sometimes up and down, in a fairly rapid motion, attracting the snake's attention. This imitated 'snake-like' movement kept the attention of the snake away from the squirrels' body and discouraged it from further 'invasion' of their activity area. The snake was slowly 'swept' away by more squirrels joining in the sweeping of tails, short low vocalizations could be heard, but no panic fleeing or running occurred. Snakes such as Cape cobras and puff adders encountered near the burrow systems were driven off in such a manner. When related to total daily activity time, defence against snakes comprised a meagre 0,5 % of total activity time.

Feeding

The major portion of active time was allocated to feeding, and was fairly constant throughout the year despite the variation in daylength. Not only did animals feed when they were sitting or standing, but also when they were digging, stopping at times during the process to sniff and then grab the bulb or root in both forepaws, eating it inside the excavation or adjacent to it. Surprisingly, the portion of feeding time did not increase during adverse periods of the year or during the harshest months of August, September and October (X^2 = 2,3; df = 2; P = 0,402) (cold-dry and hot-dry seasons (Fig. 5) as it was constant between 50 and 55 % (average 53,54 %) throughout, making up 3 to

3,5 h of all the daily activities. Digging for food comprised 12 % of the total feeding activity time and occurred most frequently during the cold-dry winter when other food sources above ground were scarce. X. inauris showed a marked tendency to take what was available, and ate new foods as soon as they sprouted. They took immature flowers and new sprouting leaves, cropping plants well before annuals were fully grown. Scatter-hoarding occurred when an excess of food such as berries or flowers was available. Buried food was never observed to be dug up again.

The use of the parasol tail could be related to season and temperature. The parasol tail activity differed significantly between seasons (X^2 = 19,995; df = 10; P = 0,005) with the highest proportion (28,0 %) occurring in the hot-dry period in comparison to 25,1 % and 17,0 % in the hot-wet and cold-dry seasons respectively. As ambient temperatures decreased (F = 11,726; df = 1; P = 0,0014) during the hot-wet and cold-dry seasons the tail-up position was used significantly less often (F = 13,11; df = 1; P = 0,0009). Soil temperatures were correlated with the tail-up position and a decline in this activity was observed as daily average soil temperatures decreased during the cold-dry season (F = 17,64; df = 1; P = 0,0002), hot-dry season (F = 6,282; df = 1; P = 0,0079) and the hot-wet season (F = 10,07; df = 1; P = 0,0028) respectively.

Resting

X. inauris lay on their stomachs in the shade of bushes and trees. Sandbathing occurred throughout the year making up to 3,0 % of the total activity time during the mid-morning (between 10h00 and 11h00) and mid-afternoon (between 16h00 and 17h00). When the data was lumped, no significant correlation with ambient temperature was detected (F = 1,923; df = 1; P = 0,1761) but the activity appeared to be significantly inversely related to soil temperature (F = 6,71; df = 1; P = 0,0148).

Table 11.   Percentage occurrence of the different locomotions of every member of the X. inauris group living at 'Rodent Hill' from August 1987 to June 1988.

ANIMAL	NO.	CLIMB	DIG	LIE	RUN	SIT	STAND	WALK	TEST
					% LOCOMOTIONS				
ADULT	♀ 1.	0,95	7,86	19,26	5,79	44,73	15,63	5,79	
ADULT	♀ 2.	1,05	7,87	20,21	5,86	44,88	14,96	5,16	NS X^2=0,909;df=6; P=0,989
SUB-ADULT	♂ 3.	0,39	7,76	22,12	4,79	46,83	13,71	4,40	NS X^2=0,912;df=6 P=0,955 SiX²=18,824;df=12 P=0,051
ADULT	♂ 6.	0,99	1,98	17,82	21,78	32,67	16,83	7,90	NS X^2=1,121;df=6 P=0,867
ADULT	♂ 7.	0,98	3,92	18,3	23,53	30,39	16,67	5,88	NS X^2=1,055;df=6 P=0,799
JUVENILES	♀ 4.	3,38	9,21	26,63	4,41	41,57	12,84	4,98	
	♀ 8.	0,50	5,61	15,89	5,14	59,31	9,81	3,74	
	♀10.	1,63	7,05	15,45	7,05	43,90	20,87	4,07	
	♀11.	1,14	8,24	6,76	9,94	44,90	17,05	2,56	
	♀13.	1,00	8,00	11,90	7,14	45,24	20,57	6,14	
	♂ 5.	1,07	8,76	27,35	3,85	41,88	11,97	5,13	NS X^2=6,859;df=6 P=0,231
	♂ 9.	0,50	9,18	19,68	2,00	45,16	20,26	3,23	
	♂12.	0,65	4,58	18,95	8,82	46,08	17,65	3,27	
	♂14.	0,50	4,44	21,72	2,22	35,56	20,00	15,56	

Basking also occurred regularly throughout the year and averaged 4,1 % of above ground activities. Most basking occurred during the cold-dry season when it comprised 6,2 % of the total activities. Basking occurred as a 'warming-up' activity when the soil and ambient temperatures during cold mornings were well below the thermo-neutral zone of ground squirrels, and when a cold wind blew. The highest frequencies were recorded between 08h30 and 10h00 in the morning and was significantly influenced by ambient and soil temperatures of the cold-dry winter period ($F=7,04$; $df=1$; $P=0,005$).

Other resting positions consisted of basking in the burrow entrance and lying on the back or stomach with the legs spread away from the body (hearthrugging). These positions made up between 22 - 28 % (average 24,25 %) of the daily above ground activities (Fig 5). During the hot-wet season 21 % of the time was spent resting compared with 26% in the hot-dry season. No specific group member rested more than another ($X^2=2,44$; df; 12; $P=0,778$). Communal sleeping occurred in the laboratory when animals were placed together in one cage and it was assumed that animals slept in groups when underground in the wild. Animals were never observed to sleep above ground.

Socializing

Two female squirrels formed the core of the group studied. The older female led the group away from the central burrow system every morning and synchronized feeding and sleeping of group members. She would also 'snarl' at the younger adult female, which was followed by anal-sniffing and especially nasal sniffing from the submissive female no 2. Two adult bachelor males were observed to visit the females on an irregular basis, probably fathering the young and then leaving again. The presence of males in the female home area elicited chasing and fighting by the older female. During such encounters sexual chasing, mounting, mating, sniffing the face and external genitalia would occur.

If both bachelor males were interested in one female, conflicts between rivals took place.

When the social activities of the adult males and females were compared, they were significantly different (X^2 = 21,327; df=3; P=0,002). Females socialized more than males did (Table 11).

When the socializing data of the various sexes and age-classes were lumped, socializing comprised between 9 and 13 % of all above ground activities; 39 to 45 min of the 6,5 h above ground. These activities did not differ significantly on a seasonal basis (X^2= 2,99; P=0,556), but an increasing social trend can be seen from the cold dry period towards the hot-wet period and was related to mating, the birth of the young and grooming offspring when above ground (Fig 5).

Grooming took place during the basking periods in the early morning and the sundown periods in the late afternoon. There was a non-significant tendency for adult females and young females allogroomed other group members more than adult males and young males did, (χ^2= 3,199;df= 3; P<0,10). This result could be a pure reflection of the males relatively short time periods spent as part of the group's general social activities. Allogrooming could not be related to any seasonal changes (χ^2 =4,38; df=3; P=0,341). Female no.2 allogroomed more than any other (X =8,78; P=0,05).

Anal sniffing was performed mostly by the older female no. 1, followed by female no. 2, (24 % versus 16 % of socializing time). Both the males anal sniffed on a regular basis for 12 % of their socializing time. No seasonal trends in anal sniffing could be found. Nasal sniffing usually occurred in conjunction with anal sniffing. Females 1 and 2 performed nasal sniffing 13,9 and 19,4 % of the total socializing time daily. Males did less nasal sniffing in comparison with the other group members; 2,8 % of the socializing time. No seasonal trends in nasal sniffing were found.

Mounting and sexual encounters were limited to four separate incidences. Both bachelor males were equally involved and only with female no. 1. Pregnant females reduced their feeding activity, actively building nests, carrying grass and other plant material in their mouths to the central burrow system before giving birth. While the young were still underground, active periods were reduced and much time was spent with them in the burrow, especially during mid day.

Behaviour patterns observed during play and fighting included circle running, loud vocalizations and tail flicking. Play occurred mostly among the young and between young and their mothers. No play differences related to the sex of the young could be identified, neither did they show a significant seasonal trend. Of the vocalizations, 26 % occurred during play. (Vocalizations are reported on in more detail under the vigilance section).

Females (1 and 2) fought against the males (6 and 7) between 42 and 45 % of the total socializing time respectively. The frequency of fighting became more intense during the hot-wet season $(X^2 = 11,23; \ df = 6; \ P=0,05)$.

Table 12. Percentage occurrence of the main X. inauris surface activities: vigilance, feeding, resting, and socializing.

| ANIMAL | NO. | % ACTIVITIES | | | | TEST |
		VIGILANCE	FEEDING	RESTING	SOCIALIZ ING	
ADULT	♀ 1.	11,61	57,85	19,12	11,42	NS; X^2=0,913; df=3; P=0,405
	♀ 2.	12,83	54,37	21,20	11,60	NS; X^2=0,888; df=3; P=0,349
SUB-ADULT	♂ 3.	11,63	56,09	23,82	8,45	NS; X^2=4,789; df=3; P=0,088
ADULT	♂ 6.	13,00	50,24	28,29	8,47	NS; X^2=0,954; df=3; P=0,198
ADULT	♂ 7.	12,02	49,23	28,18	7,22	NS; X^2=1,510; df=3; P=0,079
JUVE-NILES	♀ 4.	11,16	50,50	31,44	7,10	
	♀ 8.	11,58	60,69	20,67	7,07	
	♀10.	13,66	54,07	22,38	9,88	
	♀11.	12,84	51,99	24,77	10,40	
	♀13.	8,50	56,50	22,50	12,50	
	♂ 5.	9,43	51,26	28,02	11,29	NS; X^2=7,559; df=3; P=0,069
	♂ 9.	10,00	53,33	23,33	13,33	
	♂12.	9,38	53,47	27,43	9,72	
	♂14.	10,00	54,06	24,04	12,00	

Time spent in various states of locomotion.

Eight states of locomotion were recognised. Frequencies of the various classes of locomotion are listed in Table 11. There were no significant differences between individual squirrels within each age and sex class, however, when adult males were lumped as a group and compared to adult females, their locomotion differed significantly $(X^2 = 18,22;$ df $= 12;$ P $< 0,009)$. The males did not dig as much as the other squirrels, only on average 3 % against the $\pm$ 8,7% of the other squirrels. Being transient visitors, they interfered with the adult females, consequently adult males were frequently chased and ran more than the rest of the group members.

Most time (45,0 %) on the surface was spent sitting. Lying showed significant seasonal differences, peaking during the hot-dry season $(X^2 = 15,06;$ df $= 6;$ P $= 0,0067)$ and taking up to 24 % or 1,5 h of the above ground daytime activities. Standing followed as one of the most important locomotions used, but no significant differences between the seasons were detected. When male and female data was lumped, digging differed between the seasons peaking during the cold-dry season $(X^2 = 24,92;$ df $= 6;$ P $= 0,0001)$ at 11 %. Running occurred significantly more often during the hot-wet season $(X^2 = 24,92;$ df $= 6;$ P $= 0,0001)$, but made up a small part of the daily budget, between 5 to 11 %. Walking did not show any significant seasonal differences.

Table 13. Percentage occurrence of the seven states of locomotion during the three seasons in X. inauris. Season : CD = cold-dry; HD = hot-dry; HW = hot-wet.

LOCOMOTION	CD	HD	HW	TEST
STAND	13,1	16,9	17,5	$X^2 = 5,12$; df = 16 P = 0,0882; NS
SIT	43,1	41,4	49,3	$X^2 = 2,312$; df = 8 P = 0,9930; NS
WALK	5,0	5,0	4,8	$X^2 = 9,95$; df = 8 P = 0,4440; NS
RUN	5,4	4,9	8,9	$X^2 = 5,46$; df = 8 P = 0,0037; significant
DIG	11,2	6,9	4,3	$X^2 = 24,92$; df = 6 P = 0,0001; significant
CLIMB	1,6	0,8	0,2	$X^2 = 1,56$; df = 6 P = 0,2061; NS
LIE	20,6	24,1	15,0	$X^2 = 15,06$; df = 6 P = 0,0047; significant

Climbing was seen on rare occasions and comprised only 1 to 2 % of the daily activities with no significant difference between seasons (Table 13).

Home-area use

Home range shapes are often influenced by the topography of a study area. In this study the dome-shaped red dunes surrounding the home area had a profound influence on these shapes as squirrels preferred to forage below the dune slopes rather than on their sides or crest.

Feeding distances between individuals were significantly shorter in the hot-wet season (Table 14). During the cold-dry season, a distance of 11,7 ± 2,6 m to the closest burrow was maintained, significantly greater than in the hot-wet season when 7,4 ± 2,3 m was noted. The total group width while above ground

differed significantly seasonally and was almost twice as great during the cold-dry season than during the hot-wet season (F=15,64; df=2; P=0,0037).

Females concentrated their activities significantly closer to the central burrows than the males did (X^2=22,85; df=2; P>0,001). They concentrated their movements on the periphery of the female home area. When the adult bachelor males (no. 6 & 7) were present in the female (no. 1 & 2) area, the male areas were larger, although not significantly so (F=3,01; df=3; P=0,871). When the total area of males and females were compared, irrespective of season, males had a significantly larger home areas than females (t=-2,91; df=3,0; P<0,05). The male home range areas were not a reflection of their 'true' roaming area as they were transient, 'visiting' the females irregularly. The two adult female home areas overlapped and did not differ significantly from each other (F=9,56; df=1; P=0,06), but their home area size during the hot-dry season did differ significantly from the other two seasons (F=34,80; df=768; P=0,0001) (Table 15) (Fig. 7-12). No significant seasonal differences could be shown between home area use (F=13,0; df=2; P=0,07). The estimated home range of juveniles was between 0,95 and 4,00 ha and when the seasonal data were lumped, juvenile males did not have significantly larger home areas than young females (t=-1,69; df=7; P=0,885).

Table 14. The foraging width, individual distance and distance (m) from the closest burrow of X. inauris while active above ground, during the three seasons. CD=cold-dry; HD=hot-dry; HW=hot-wet.

FORAGING	SEASONS			TEST
	CD	HD	HW	
DISTANCE CLOSEST INDIVIDUAL	10,5 ± 5,5	4,7 ± 1,8	1,6 ± 0,8	F=147,18; df=2; P= 0,0001
DISTANCE CLOSEST BURROW	11,7 ± 2,6	8,4 ± 2,7	7,4 ± 2,3	F= 54,75; df=2; P= 0,0001
GROUP WIDTH	21,7 ± 4,8	16,3 ± 3,1	12,4 ± 3,7	F= 15,64; df=2; P= 0,0037

The first week or two after initial emergence, juveniles usually remained within a few metres of their natal burrow (or an adjacent entrance). After two weeks they began moving an average of $8 \pm 2,1$ m from the burrow.

Table 15. The home ranges (ha) of X. inauris as estimated by the minimum area method. CD=cold-dry season; HW=hot-wet season; HD= hot-dry season.

Squirrels	N	Seasons		
		CD	HD	HW
Adult females	2	4,55 $\pm$ 0,10	8,55 $\pm$ 2,50	5,35 $\pm$ 0,10
Adult males	3	6,00 $\pm$ 1,50	10,50 $\pm$ 2,50	4,00 $\pm$ 2,50
Young females	5	2,005 $\pm$ 0,01	4,00 $\pm$ 0,10	0,95 $\pm$ 0,06
Young males	4	1,905 $\pm$ 0,01	3,90 $\pm$ 0,05	1,84 $\pm$ 0,05

Fig. 7-12 illustrates the female and juvenile home range areas that was analysed to reveal patterns of range use. During the cold-dry season females and juveniles used 22,0 % of the total home area (contained 95% of all locations) (Fig. 7 and 10). During the hot-dry season, the home area use by females was higher than for the juveniles and only 3,6 % of total area when 95% of the locations are measured was used, indicating that the young used probably only the small area surrounding the central burow system (Fig 8 & 11).

max area 2.465 ha.
Clustered areas :

```
%    ha    (%max)   nuc.                           cold-dry
95   0.64  (25.96)  56
90   0.56  (22.72)  56
85   0.56  (22.72)  56
80   0.56  (22.72)  56
75   0.56  (22.72)  56
70   0.56  (22.72)  56
65   0.56  (22.72)  56   100
60   0.56  (22.72)  56
55   0.56  (22.72)  56
50   0.56  (22.72)  56%Ar
45   0.56  (22.72)  56
40   0.56  (22.72)  56
35   0.56  (22.72)  56   50
30   0.56  (22.72)  56
25   0.56  (22.72)  56
20   0.48  (19.47)  48
```

```
        0
        100   90   80   70   60   50   40   30   20
                    % Points in clusters
```
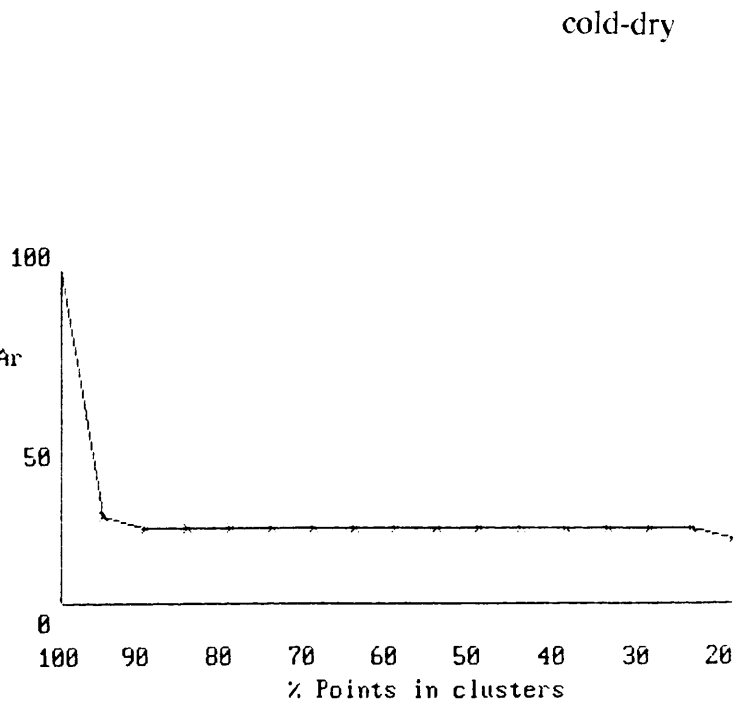
Fig. 7. The utilization distribution by cluster analysis of all X. inauris juveniles during the cold-dry season at 'Rodent Hill'. % Ar = Percentage area.

max area   4.67 ha.
Clustered areas :

%	ha	(%max)	nuc.
95	0.69	(4.70)	55
90	0.53	(3.61)	53
85	0.53	(3.61)	53
80	0.53	(3.61)	53
75	0.53	(3.61)	53
70	0.53	(3.61)	53
65	0.53	(3.61)	53
60	0.53	(3.61)	53
55	0.53	(3.61)	53
50	0.53	(3.61)	53%Ar
45	0.53	(3.61)	53
40	0.53	(3.61)	53
35	0.53	(3.61)	53
30	0.53	(3.61)	53
25	0.53	(3.61)	53
20	0.48	(3.27)	48

hot-dry

% Points in clusters
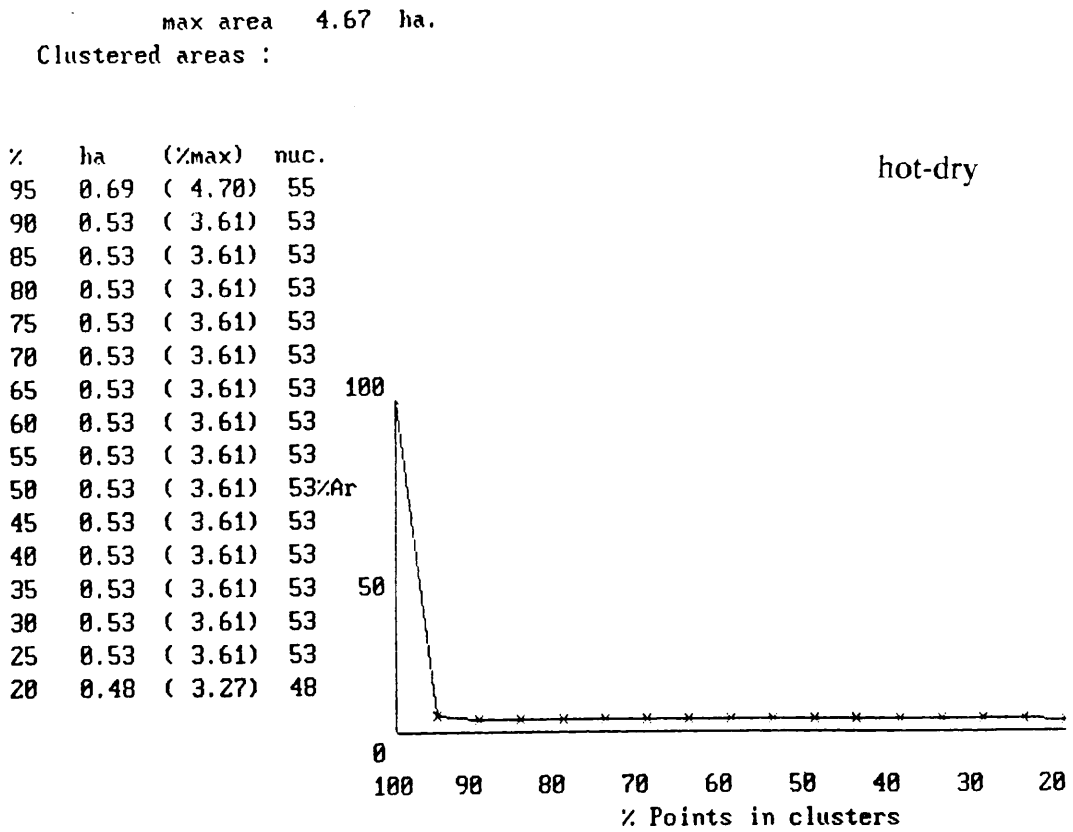
Fig. 8. A utilization distribution by cluster analysis of all _X inauris_ juveniles during the hot-dry season of 1987 at 'Rodent Hill'. % Ar = Percentage area

max area 1.855 ha.
Clustered areas :

%	ha	(%max)	nuc.
95	0.49	(26.42)	35
90	0.33	(17.79)	32
85	0.32	(17.25)	32
80	0.32	(17.25)	32
75	0.32	(17.25)	32
70	0.32	(17.25)	32
65	0.32	(17.25)	32
60	0.32	(17.25)	32
55	0.32	(17.25)	32
50	0.32	(17.25)	32%Ar
45	0.32	(17.25)	32
40	0.32	(17.25)	32
35	0.32	(17.25)	32
30	0.32	(17.25)	32
25	0.32	(17.25)	32
20	0.32	(17.25)	32

hot-wet

% Points in clusters
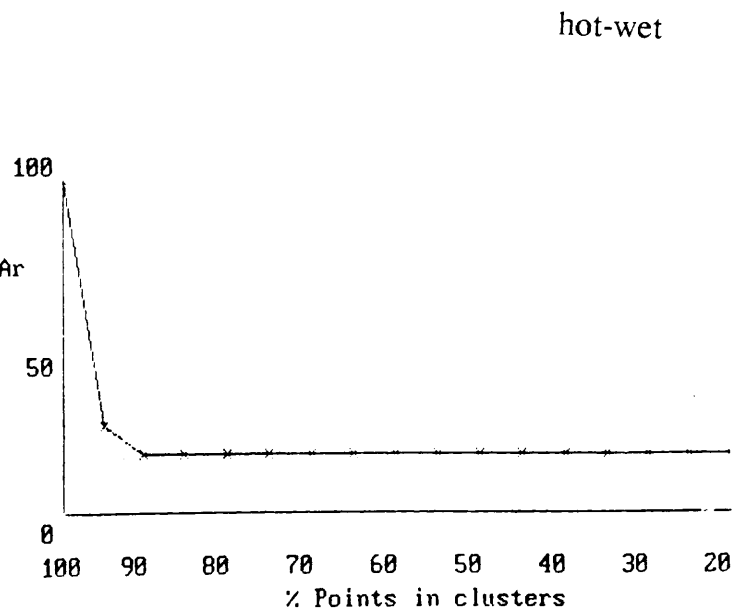
Fig. 9. A utilization distribution by cluster analysis of all X. inauris juveniles during the hot-wet season of 1987/1987 at 'Rodent Hill'. % Ar = percentage area.

max area 4.415 ha.
Clustered areas :

```
%     ha     (%max)   nuc.
95    0.57   (23.60)   54
90    0.54   (22.36)   54
85    0.54   (22.36)   54
80    0.54   (22.36)   54
75    0.54   (22.36)   54
70    0.54   (22.36)   54
65    0.54   (22.36)   54    100
60    0.54   (22.36)   54
55    0.54   (22.36)   54
50    0.54   (22.36)   54%Ar
45    0.54   (22.36)   54
40    0.54   (22.36)   54
35    0.54   (22.36)   54    50
30    0.54   (22.36)   54
25    0.54   (22.36)   54
20    0.51   (21.12)   51
```

cold-dry

```
0
100  90   80   70   60   50   40   30   20
        % Points in clusters
```
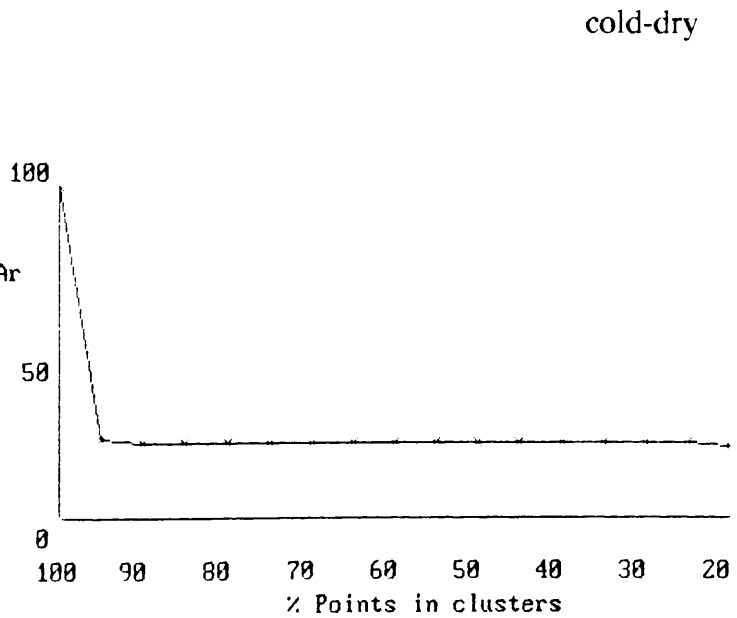
Fig. 10. A utilization distribution by cluster analysis of both X. inauris females during the cold-dry season of 1987 at 'Rodent Hill'. % Ar = Percentage area.

max area 8.695 ha.
Clustered areas :

%	ha	(%max)	nuc.
95	8.47	(27.73)	46
90	8.46	(27.14)	46
85	8.46	(27.14)	46
80	8.46	(27.14)	46
75	8.46	(27.14)	46
70	8.46	(27.14)	46
65	8.46	(27.14)	46
60	8.46	(27.14)	46
55	8.46	(27.14)	46
50	8.46	(27.14)	46%Ar
45	8.46	(27.14)	46
40	8.46	(27.14)	46
35	8.46	(27.14)	46
30	8.46	(27.14)	46
25	8.46	(27.14)	46
20	8.46	(27.14)	46

hot-dry

% Points in clusters
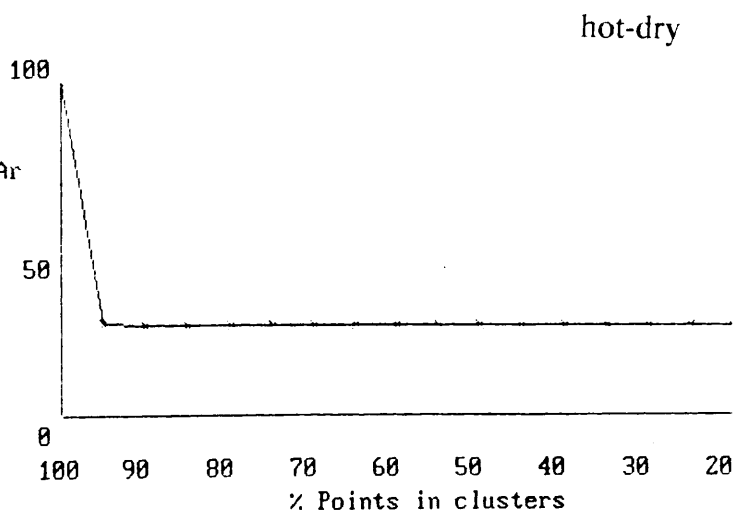
Fig. 11. A utilization distribution by cluster analysis of both X. inauris females during hot-dry season of 1987 at 'Rodent Hill'. % Ar = Percentage area.

max area 5.495 ha.
Clustered areas :

%	ha	(%max)	nuc.	
95	0.66	(12.01)	60	
90	0.57	(10.37)	57	
85	0.57	(10.37)	57	
80	0.57	(10.37)	57	
75	0.57	(10.37)	57	
70	0.57	(10.37)	57	
65	0.57	(10.37)	57	100
60	0.57	(10.37)	57	
55	0.57	(10.37)	57	
50	0.57	(10.37)	57%Ar	
45	0.57	(10.37)	57	
40	0.57	(10.37)	57	
35	0.57	(10.37)	57	50
30	0.57	(10.37)	57	
25	0.57	(10.37)	57	
20	0.52	(9.46)	52	

hot-wet

% Points in clusters
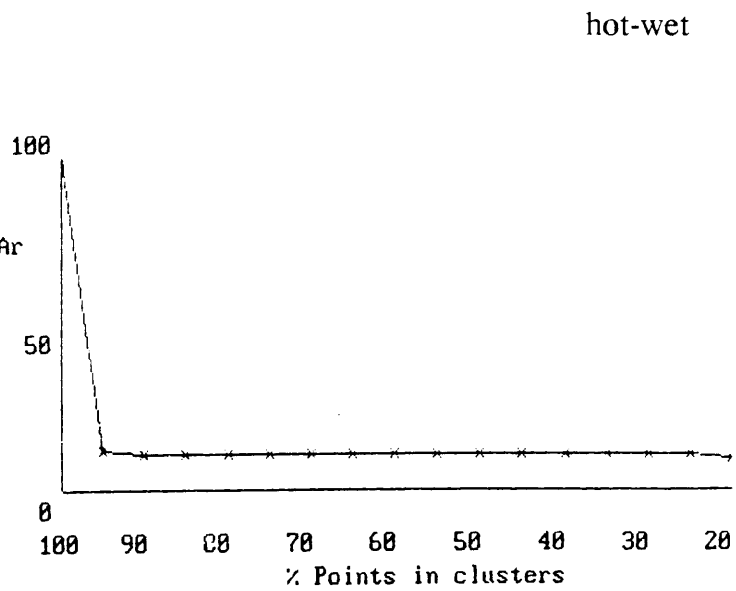
Fig. 12. A utilization distribution by cluster analysis of both X. inauris females during the hot-wet season of 1987/88 at 'Rodent Hill'. % Ar = Percentage area.

DISCUSSION

Temporal patterning of activities

The amount of time an animal devotes each day to different activities is a common measurement in behavioural ecology. It is a prerequisite for the development of time-energy budgets and a requirement for testing optimal foraging theory. As season and habitat utilization affect time budgets, these factors might be expected to be related to thermal regulation which in part is a function of body size (Belovsky 1984).

For other squirrel species (Aschoff 1981, Tonkin 1983), daybreak acts as a time-setter for the onset of the active phase of the endogeneous cycle. However, X. inauris activity patterns revealed no apparent 'Zeitgeber-entrained' surface-activity rhythms. Instead, it is proposed that daily decisions are made on when to begin and terminate activity based on appraisal of environmental conditions and on external and internal dynamic states (e.g. nutritional requirements, food-item density) and on experience of their home-area. Photoperiod seemed to have played a minor role as activity did not necessarily start an hour after first light but was influenced by factors such as temperature and wind speed. Photoperiod manipulation experiments on captive squirrels might confirm this speculation. Morning activities did not start at daybreak when dense cloud cover, low ambient temperatures and a strong wind prevailed. Cloud-cover in the present study appeared to exert its main effect through delaying first light by as much as an hour, usually with lower temperatures. Normal activities were discontinued during heavy rainfall, but if drizzle was experienced squirrels were active, emerging from the central burrow for short bouts. Similar results were found for other squirrels (Tittensor 1970). In large nocturnal rodents such as porcupines (Hystrix africae-australis) (Alkon & Saltz 1988) and giant rats (Cricetomys gambianus) (Knight 1984) activity was also influenced by these climatic factors. High winds and dust storms inhibited any X. inauris activity

and only when these winds continued for more than a day did squirrels emerge for short feeding spurts.

The bi-phasic activity cycle of X. inauris of 6 - 7 h above ground activity, has also been found in red squirrels (Sciurus vulgaris) (Tonkin 1983), golden-mantled squirrels S. saturatus (Kenagy, Sharbaugh & Nagy 1989) and Psammomys obesus, a diurnal desert sand rat (Ilan & Yom-Tov 1990). Climatic factors, specifically those of the thermal environment, were probably the direct cause of the biphasic activity pattern with a siesta period when temperatures rose too high and became a physiological burden. Whenever temperatures were above 36° C or below 15° C, squirrels would take refuge underground where temperatures, although following above ground tendencies, were more stable (Chapter 2; Chapter 5). In summer and even during winter, activity preceded or followed the hot hours of the day. It can be an advantage to escape the heat during midday, avoiding a thermoregulatory response and concomitant water loss.

Feeding

Feeding, the major component of above ground activities' made up to 52,0 % of the total activity. Although no significant seasonal differences occurred, feeding time tended to be longer when food was relatively scarce and of lower quality during the cold-dry and hot-dry seasons and shorter during the hot-wet period when food was plentiful, energy rich, and easily found. Similarly other squirrels such as S. vulgaris (Tonkin 1983) and golden-mantled squirrels (S. saturatus) (Kenagy et al. 1989) showed seasonal feeding shifts as a result of changes in food quality and quantity.

The annual feeding pattern could be divided into two periods. For the first four to five months after the summer rains (falling usually between December and April) nutrient constraints appeared to be relatively unimportant. During the

spring, when the first rains fell, squirrels fed on highly digestible plant tissues with adequate water and high nitrogen content (Chapter 3). However, when the vegetation started to dry out in the extended winter months (August, September), X. inauris resorted to digging and took termites (Hodotermies) whenever available during the first short spring storms of September 1987.

X. inauris forage from their central burrow-system and can be called central-place foragers, not leaving their home area at times when food is scarce, using the area surrounding the central burrow intensively and always returning to the central burrow-system. Instead of losing time and energy to search for better food sources further afield from the central burrow and the simultaneous possibility of being compromised by a predator, they rather used another dimension of their environment and dug for bulbs and roots. Digging was more common during the dry seasons of the year. However, X. inauris males, travelled further on foraging trips and concentrated their activity further from the burrow than the females.

The use of their parasol tails for shading could also be very important while feeding, as it possibly gave squirrels longer hours above ground plus the possibility of foraging in the open at high ambient temperatures where no vegetation shade is found. Bennett et al. (1984) estimated that up to 5,0 % of their thermoregulatory energy was saved by using the tail as a parasol.

From a classical optimal-foraging perspective (Pyke 1984), X. inauris possess traits associated with time minimizing and energy maximizing : 1) they take a variety of foodstuffs from roots, bulbs, leaves and flowers to berries and, when available, termites (Chapter 3); 2) they have a unilocular hemiglandular stomach and adaptable fermentative caecum (Chapter 6); 3) they generally use all hours of daylight, apart from very hot or cold periods, to forage and possibly make use of their parasol tail to extend foraging time; 4) they are vulnerable to a wide variety of predators.

Vigilance

Predator avoidance is important, as death is the ultimate loss of fitness (Pyke 1984). Apart from the thermoregulatory advantages of the bristly, shiny khaki coloured pelage, its colouration probably gives a cryptic advantage to individuals. However, X. inauris avoid predation by means of overt vigilance, vocalizations, use of tail-flicking and immediate escape into the closest burrow. Selective pressures suggested to have led to group living are primarily predation, food exploitation and extreme resource partitioning (Armitage 1981). Communication between group members has important consequences: it allows members of a group to co-operate with one another, but to a lesser degree also to exploit each other. Grouping can improve detection of enemies and each individual has a smaller chance of being attacked; the dilution effect (Hamilton 1971, Dehn 1990). All squirrel group members were equally vigilant. The flight-distance from predators was on average 65 ± 15 m; raptors initiated flight earlier than ground-dwelling predators such as jackals. As up to 1 burrow /2200 m^2 was available in the home range area to the squirrels, risk of being caught was reduced. Signals such as tail flicking, 'freezing' and vocalizing enhanced escape and no successful attacks were observed. Such vocalizations have been observed for Spermophilus beldingi (Sherman 1977) and not only alerted members of their own species but also other animals of an impending danger, and calls deterred predators from actually attacking. In X. inauris it was noticed that the alarm calls function to help the group or to warn reciprocators such as the whistling rats (P. brantsi), yellow mongooses (C. pencillata) and suricates (S. suricata), apart from having a function of warning kin, as was found by Sherman (1977). Therefore nepotism or favouritism is not only limited to parental care but can also be seen in alarm calls alerting adults and offspring.

The successful 'snake-directed' mobbing of X. inauris confused the snake, as squirrels immitated a snake-like movement using the sideways tail movement. Furthermore, the snake was discouraged of further hunting in the area and therefore it served the purpose of protecting the young. These mobbing

phenomena were discussed by Curio and Vieth (1978) and fits some of the listed functions of mobbing.

The positive correlation of raptors seen in the squirrel home area with rainfall gave a clear indication why squirrels were more vigilant during the hot-wet season. Group foraging widths were smaller during the hot-wet season when cover improved and, apart from individuals being closer spaced, predators were detected and avoided under these circumstances more easily. Like prairie dogs (C. ludovicianus) opening the environment around colonies by feeding near the central burrow especially the thick vegetation resulting from summer rains, thereby improving detection of predators (King 1955), X. inauris also cleared the thick vegetation resulting from summer rains by intense feeding around their central burrow system. On the other hand, predators were able to detect their prey better. The possiblity that the clearing action could be connected with removing obstacles in squirrel flight paths could not be denied.

Sociality

Armitage (1981) defined sociality as the state of group formation where members of differing sex and age shared similar dimensions of space. X. inauris could possibly be classed as egalitarian polygynous coteries (Michener 1983). Groups of squirrels formed 'aggregations' and not true social groups and were characterized by dominance relationships. Males seem to maintain areas encompassing several female groups and were sometimes clustered together as bachelor groups (Chapter 3).

Easily defendable resources are those which are predictable in time and space. If the cost of defending an area overrides the benefit of keeping such an exclusive area it is not worthwhile protecting it. No direct evidence of territoriality, that is active aggression or defence of the home area against other squirrels was observed. However, scent-marking with urine (as urine dribbling

occurred in captivity) and pedal-gland secretions could possibly provide subtle messages to other adjacent squirrel coteries, but whether such behaviour can be related to territoriality has yet to be shown. Sciurus species have extensive overlapping home-ranges without any exclusive territorial areas (Harestad & Bunnell 1979). However, T. hudsonicus (Rush & Rheeder 1978) have been found to be strictly territorial.

In the Kalahari, young ground squirrel males seem to disperse during late summer prior to reaching reproductive maturity. Social 'rank' amongst the squirrel group members is present, but could not be followed as this study was not study designed to detect the differences in social order. However rank seemed to be established by fighting, bluffing and threat during daily encounters and reinforced at subsequent involvement. Most fighting, sexual, and allogrooming encounters took place during the hot-wet season.

Spatial use

Home range area indicates the undefended area used by an animal during its routine activities (Calhoun & Casby 1958) and can be calculated in a variety of ways as reviewed by Macdonald, Ball & Hough (1980) and Bergstrom (1988).

Using the minimum area method poses problems :1) locations must be independent; 2) all except the peripheral locations are ignored; 3) the system is sensitive to long range short duration bouts; and 4) area estimates are dependent upon sample size (Don 1983). However in the present study, the method gave an estimate of total area use and sample sizes were large (Table 15).

Home range sizes are usually inversely related to food availability (Rusch & Reeder 1978, Lewis 1982, Mace & Harvey 1983, Waterman 1986, Herrera & Macdonald 1989, McNab 1989). X. inauris seems to be non-territorial with

overlapping home ranges, with several animals having access to the same food supply. They do not hoard their food in their burrows, although scatter-hoarding has been observed.

Within a specific trophic group and weight class, habitats of greater productivity generate smaller home ranges, but the effect of plant dormancy on the home area size would have opposite effects (Harestad & Bunnell 1979). X. inauris occupy a three-dimensional environment; with climbing and especially digging being important and, when considerations of space-use, one must include these factors. Home range size changed for X. inauris during the present study and correlated with food needs and availability. Since little vegetation and low cover (Appendix 1), (the latter enhanced by the fact that the area surrounding the central burrow system was stripped of vegetation during the cold-dry and hot-dry seasons), influenced the size of the inhabited area, on average squirrels had larger home areas of 7,4 $\pm$ 2,6 ha during winter and early summer than during mid-summer (3,85 $\pm$ 0,48 ha) (Table 15). The home ranges of X. inauris at Rodent Hill were similar to those of squirrels such as Spermophilus carolensis (0,9 ha to 5,0 ha) (Harestad & Bunnell 1979) and Spermophilus variegatus (7,9 ha) (Ortega 1990). These squirrels were of similar body size and lived in similar habitats with common characteristics such as low plant productivity and cover. Sciurus griseus, another herbivorous squirrel of similar mass to X. inauris, lives in more mesic environments and has much smaller home ranges of 0,30 ha (Mohr 1947). Similarly, the two arboreal squirrels Paraxerus ornatus and Paraxerus tongensis living in tropical mesic forests, both had home ranges of 2,7 ha each (Viljoen 1980). These home areas were smaller than X. inauris's home areas, probably as a consequence of their arboreal way of life and higher food densities. Don (1983) plotted five tree squirrel home range areas against body mass and found that the data varied considerably and no relation could be drawn between home area and body mass. These similarities and contradictions make comparisons ambiguous, even between members of the same family like the Sciuridae, and other variables such as sociality, predator avoidance, feeding

patterns and arborial or terrestrial modes of life play profound roles in the comparisons and trends (Harvey & Clutton-Brock 1981).

The 'natal' dispersal to new home ranges found in Columbian ground squirrels (Spermophilus columbianus) (Wiggett & Boag 1989) was not observed in X. inauris and a longer extensive study period is necessary to confirm or deny this. X. inauris males seem to disperse as yearlings, as found for Columbian and Richardsons' ground squirrels (S. columbianus) (Waterman 1986). Sex differences in use of space and social behaviour seemed to develop relatively later in X. inauris than in other ground squirrels. 'Kin-clusters' of ground squirrel females and daughters appeared to be linked to the central or natal burrow system and have been described as a general shaping factor in squirrel social organizations (Armitage 1981, Michener 1983, King 1989). X. inauris juveniles had very small home areas as dispersal and joint foraging bouts were only initiated when they were about four to five months old. The phenomenon of males using larger home areas than females was also found for S. carolensis (Thompson 1982) and S. vulgaris (Tittensor 1970).

Home range size and movements above ground increased in adult females of S. variegatus and a variety of sciurid species following the emergence and subsequent independence of the young (Michener 1983, Ortega 1990). Male squirrels are known to move over larger areas in search of oestrous females. Likewise, X. inauris bachelor males seem to roam over large areas visiting females of different home coteries. Utilization distribution of space is illustrated in Fig 7- 12. These space distributions are uniform, but some parts of the home areas were rarely visited. The activities of young and adult females were mainly from and around the central burrow system. The males used several other areas surrounding the females home-area and the intensity chart of their use only reflects the use of the area on irregular occasions and was not included.

Summary

X. inauris are active above ground for 6 to 7 h a day, with feeding and resting being the most important activities. Seasonal trends influenced their bi-phasic day, having longer siesta periods during the summer periods than the winter period. Environmental factors such as ambient temperature, soil temperature, cloud cover, wind and rain also had significant effects on daily activities. Food availability played an important role in foraging activities. Foraging took place for longer periods and further from the central burrow system during the cold-dry season. More digging took place in the hot-dry season when surface food became depleted. It is suggested that X. inauris are energy maximizers and time minimizers. All squirrels were equally vigilant and there were some seasonal effects on vigilance, which could be correlated with the higher raptor numbers found in the hot-wet season. X. inauris formed family coteries with the home range area (3 - 7 ha) of the group enlarging during the winter period, comparable to other squirrels living in dry habitats. No definite territorial behaviour was seen. Females were more social than males and an alpha female appeared to dominate the group. Females concentrated their activities closer to the central burrow system during the breeding season (hot-wet).

CHAPTER 5

THERMOREGULATION   IN SINGLE AND GROUPED SQUIRRELS

INTRODUCTION

Rodents are amongst the most successful mammals occurring in arid areas (Hart 1971, Grodzinski & Wunder 1975). Despite the climatic extremes in arid regions, small mammals do not have to live in the meteorological environment of unpredictable rainfall and excessive high summer and low winter temperatures. Through natural selection, animals evolved so that their physiological capacities could cope with the conditions (Schmidt-Nielsen 1983, Louw & Seely 1982, Dawson et al. 1989).

Birds and mammals have escaped environmental constraints by evolving a thermoregulatory system of endogeneous heat production, and this exchange of heat is largely under physiological control. Most endotherms have a narrow range of body temperatures within which they can survive. Consequently temperature regulation takes up time and metabolic energy reserves, sometimes under harsh circumstances (Bartholomew 1964). In order to provide some background for an understanding of thermoregulation in rodents, it is necessary to examine the actual environmental conditions of the habitat, thermal conditions of the microclimate, as well as the physiological responses of heat production and loss under extreme and 'normal' circumstances.

To determine whether thermoregulatory adjustments to environmental conditions are intertwined with behaviour and ecology, the small, diurnal X. inauris, offers an attractive opportunity to examine metabolic capabilities under adverse conditions.

Gordon, Fehlner & Long (1986) emphasised that most mammals evolved preferred ambient temperatures (T_a) to avoid autonomic thermoregulation by

employing behavioural adaptations as an alternative. Although X. inauris inhabit burrow systems, thus avoiding the extremes of hot and cold in summer and winter, and makes use of an array of thermoregulatory behavioural patterns, little is known about the extent to which their autonomic thermoregulatory mechanisms and behavioural reactions vary seasonally.

Sciurid rodents from other regions of the world occupying xeric environments, show a variety of physiological adaptations including lower than expected metabolic rates, increased tolerance to high ambient temperatures (T_a), and increased tolerance to elevated body temperatures and hibernation (Hudson & Deavers 1973, Chappell & Bartholomew 1981, Reynolds 1985).

Energy metabolism of the four southern African tree squirrel species was investigated by Viljoen (1985). Although all the arboreal species are adapted to hot regions, the forest dwelling species were stressed at T_a's above 34° C, contrary to the savanna species. Haim et al. (1987) compared thermoregulation between X. inauris and X. princeps. None of the parameters they tested identified significant physiological differences, but both species showed ; 1.) hyperthermia commencing within the TNZ (thermal neutral zone) ; 2.) low resting metabolic rates (RMR) and higher conductances than expected for their body masses.

X. inauris is colonial (Herzig-Straschil 1979), building extensive burrow systems of up to 800 mm deep in open areas within hard surfaces such as riverbeds, pans, incipient pans and dune-streets (Chapter 3). The study area was characterized by extreme heat in summer with day temperatures averaging $\pm$ 36° C and often sub-zero temperatures in winter (Chapter 2). Nevertheless, X. inauris showed no signs of aestivation or hibernation.

Total energy expenditure for many small mammals, is a major factor in winter. This cost will be especially important to squirrels such as X. inauris which spend $\pm$ 6 h above ground during winter days (Chapter 4). Although the winter

temperatures of burrow systems follow above ground temperatures, these burrows are environments of almost constant temperature and provide suitable thermal from extremes of cold and hot. The usual vertical thermal gradient within burrow systems provides the possibilty for rodents to select a location in the burrow at which thermal stress would be minimal (Kay & Whitford 1978). However, minimum ambient temperatures of 7 °C have been measured in X. inauris burrows during winter, which could pose thermoregulatory problems for squirrels. Successful reduction of nocturnal energy expenditure would probably depend to a large extent on behavioural and to a lesser extent on physiological adjustments. Such adjustments will either reduce heat loss or increase heat production during exposure to cold. For example huddling is considered to be of major significance for small social mammals to save energy (Pearson 1960, Sealander 1952, Gebezynski 1969, Mount 1960, Withers & Jarvis 1980, Vogt & Lynch 1982, Karasov 1983b). Hart (1971) reported that when mice huddle in a nest their own ambient temperature is elevated to such an extent that a metabolic response to cold is not necessary. The physiological effect of huddling in the naked mole-rat lowered mass-specific thermal conductance by 48 % (Withers & Jarvis 1980). The rate of heat loss of huddled animals would be proportional to surface area. By increasing body mass but proportionally diminishing surface area by a few huddling individuals, less energy would be needed to regulate body temperature. This saving is hypothesised to be of benefit especially during winter when food quality is low. This is further enhanced by the squirrels relatively large body size. This study therefore investigated whether huddling in X. inauris functions as a thermoregulatory behavioural mechanism.

Small mammals are exposed to a variety of seasonally changing stimuli apart from temperature. It is furthermore, well known that acclimated squirrels may not reflect the natural state of the environment. For this reason several workers preferred to make use of acclimatized animals in their laboratory studies such as done by Wunder, Dobkin & Gettinger (1977) who measured seasonal thermogenesis shifts in acclimatized prairie voles (Microtus ochrogaster). Pauls

(1981) did a thermoregulatory study on acclimatized red squirrels (Tamiasciurus hudsonicus). Karasov (1981) used acclimatized antelope ground squirrels (Ammospermophilus leucurus) when testing their daily energy expenditure. Likewise Ducharme, Larochelle & Richard (1989) tested the thermogenic capacity of acclimatized gray squirrels (S. carolensis). Here it was therefore decided to make use of acclimatized squirrels and not to acclimate squirrels, as thermogenic responses would then be exposed to one or two extrinsic stimuli only.

This chapter examines the thermoregulatory and energetic responses in single acclimatized X. inauris at temperatures below the TNZ established by Haim etal. 1987 to determine the possible importance of being diurnal in the face of being of a relatively large size. These aspects will then be studied in conjunction with the possible importance of burrows, use of above-ground shade and posture during the year; and group huddling as thermoregulatory measures.

MATERIALS AND METHODS

X. inauris were trapped at Nossob camp in the Kalahari Gemsbok National Park, South Africa (25° 25' S; 20° 36' E). The seasons can be divided into the cold-dry winter (May-August), the hot-dry summer (September-November) and hot-wet summer (December-April). Squirrels were caught during the cool-dry and hot-wet seasons for the respective seasonal experiments. For more details on the average maximum and minimum daily temperatures vide Chapter 2.

Six hot-wet acclimatized animals (three males; three females) with a mean body mass of 547,46 ± 27,84 g and six cold-dry (three males; three females) acclimatized squirrels with a mean body mass of 559,88 ± 37,66 g were taken directly from the field to the laboratory during January and June 1987 respectively. Animals were housed singly under prevailing natural photoperiod,

in stainless steel cages and fed a dry rodent diet consisting of pronutro (Cerebos Food Corp. Ltd., Wadeville, South Africa), carrots, apples and sunflower seeds. Shredded paper was provided for bedding. Animals were not starved before experiments as they tended to be restless under fasting conditions. All oxygen consumption experiments on individual squirrels were conducted within seven days of arrival at the laboratory.

For the huddling experiment a further six (three males; three females) winter acclimatized ($\pm$ 20°C maximum) squirrels with a mean body mass of 584,51 $\pm$ 23,82 were taken directly from the field to the laboratory in July 1987, where huddling experiments without nesting material commenced immediately. In August 1988, a further six winter acclimatized squirrels (three males; three females) with a mean body mass of 588,05 $\pm$ 18,67 g were taken from the field to the laboratory for more huddling experiments. But these squirrels, were provided with nesting material. Groups of two, four or six individuals were measured to see the influence of group size on oxygen consumption.

All experimental procedures were conducted during the light phase of the daily photoperiodic cycle. Oxygen consumption rates (VO_2) of single animals were determined at six ambient temperatures, ranging from 10° C to 38° C, while groups of two, four or six squirrels were exposed to six different ambient temperatures (T_a) ranging between 10° C to 29° C. An open-circuit system was used (Decopas & Hart 1957). Single squirrels were housed in a 2,8 l cylindrical respirometer, with a perforated plastic floor on which the animal rested. During each trial, the respirometer was submerged in a regulated water bath, which maintained chamber temperature to within 0,2° C of that required, and air was provided at 1015 ml/min. Compressed air was initially dried through columns of silica gel (Unilab, Johannesburg) before entering the respirometers.

Groups of squirrels were experimented upon in a 350 l respirometer (500 x 700 x 1000mm) supplied with air at 1600 ml/min. Temperature controlled water was pumped through a network of copper piping within the chamber wall to regulate

the internal T_a to within 0,2°C. A perforated 2,8 l up-side-down asbestos flower pot with an opening of 100 x 80 mm was placed within the cage to house the huddled animals. Experiments on groups of two, four and six squirrels were conducted and with (for which shredded paper was provided) or without nesting material.

Excurrent air was passed through columns of silica gel for both the single and group experiments before entering an Applied Electrochemistry S-3A/1 single-channel oxygen analyser (Scientific Associates, Cape Town). Respirometer temperatures were determined with a Fluke 52K/J thermometer using a chromel-alumel thermocouple. This same thermometer was used to measure body temperatures (T_b) of squirrels before and after each VO_2 trial by inserting the thermocouple, lubricated with petroleum jelly, approximately 30 mm into the rectum. All animals were exposed to the experimental T_a for 1,5-2 h in the dark prior to recording. Only resting animals' oxygen consumption readings were recorded every three min. The resting metabolic rate (RMR) of each trial was taken as the mean VO_2 value that was repeatable for not less than 15 min and which did not differ by more than 0,02%. VO_2 was calculated according to Decopas & Hart (1957) and corrected to standard conditions (STP). Data are presented as the mean $\pm$ SD mass specific RMR (ml O_2/ g/h) of all animals tested at each ambient temperature. Conductance (C) below the lower critical temperature (T_l) was calculated from individual measurements of VO_2/M (where M = mass in g) using the formula C = $(VO_2$/M)(Tb-Ta) (Hart 1971), where C is measured in ml O_2/g/°C/h. If the animals became active during the recording period the results were discarded.

Evaporative water loss (EWL) (from pulmacutaneous evaporation of grouped squirrels only) into dry air was collected in a pre-weighed column of silica gel, which was later re-weighed to the nearest 0,1 mg. Several readings of the dorsal, ventral and tail hair length were recorded with calipers from animals captured for the seasonal experiments.

The behavioural study was conducted using the five-minute scan sampling procedure to record all activities of individuals (Lehner 1979) (Chapter 4). The environmental and burrow temperatures were recorded at Nossob camp and are discussed in more detail in Chapter 2. During road counts of animals, done by the research officer, M. H. Knight in the Kalahari Gemsbok National Park, group sizes of X. inauris were noted on a two-monthly basis from a four-wheel drive vehicle over a five-year period.

All data are presented as means $\pm$ SD. Regression analyses were calculated using the method of least squares (Runyon & Haber 1980). The data were tested for significance using ANOVA and Student's t-tests (SAS 1988).

RESULTS

Thermoregulation in single squirrels

Below the TNZ (Haim etal. 1987), summer acclimatized squirrels had a significantly higher (t=2,88; df=10; P<0,05) mean T_b 35,75 $\pm$ 0,21 ° C in comparison to the 35,17 $\pm$ 0,16 ° C of winter acclimatized animals. In summer and winter acclimatized squirrels T_b could be described by:

$$y = 33,7 + 0,14x; \quad r = 0,89 \quad (n=24) \quad (P<0,001)$$

and

$$y = 34,8 + 0,11x; \quad r = 0,68 \quad (n=24) \quad (P<0,001)$$

respectively, where $y = T_b$ and $x = T_a$.

As the differences between T_a and T_b decreased the conductance (C) increased. Above 33° C, the C increased for both summer (66 %) and winter (64 %) acclimatized squirrels to 0,3218 $\pm$ 0,075 and 0,3897 $\pm$ 0,158 ml O_2 /g/ h/° C respectively (Fig 14).
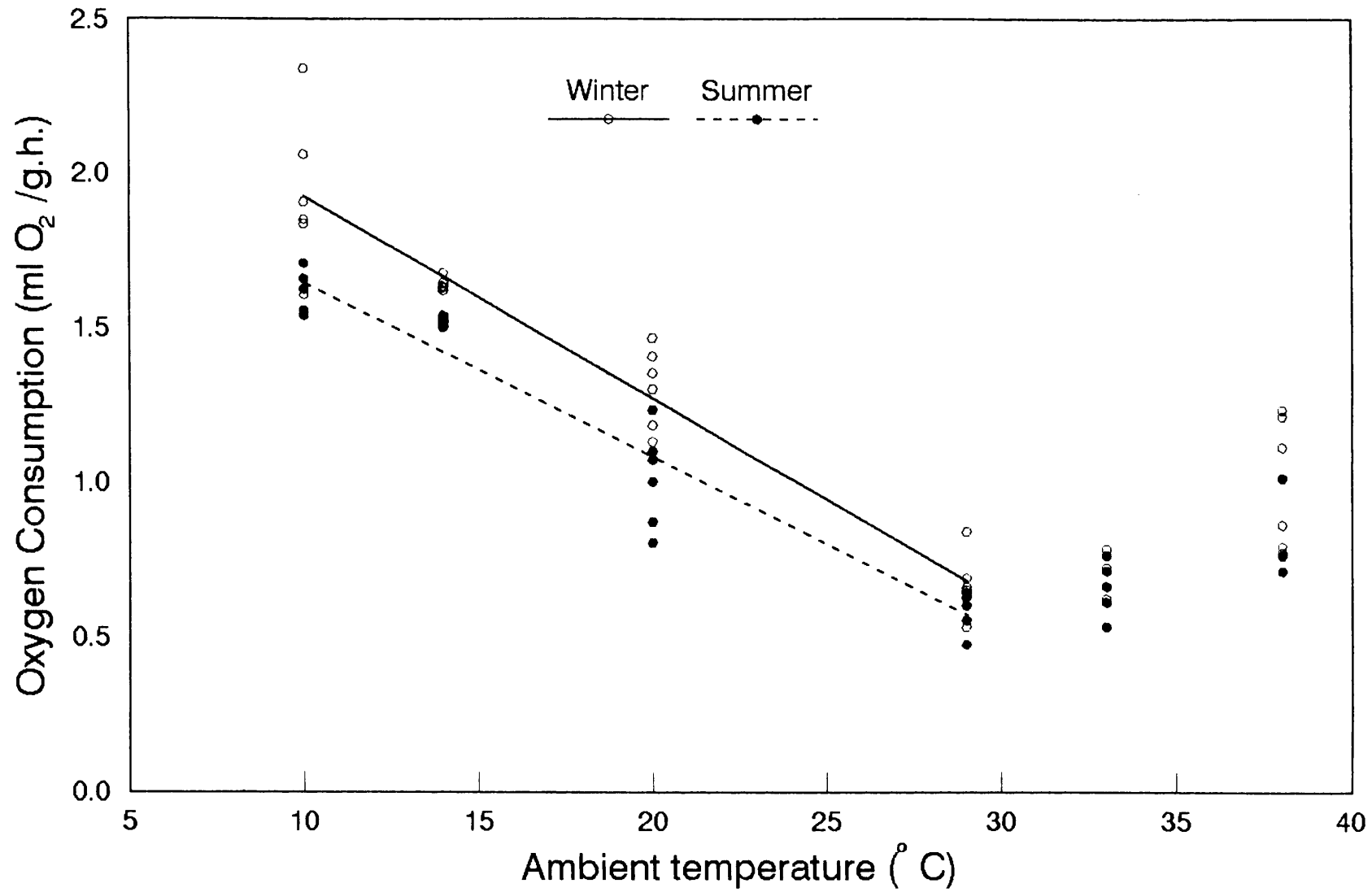
Fig. 13. Oxygen consumption of summer and winter acclimatized X. inauris
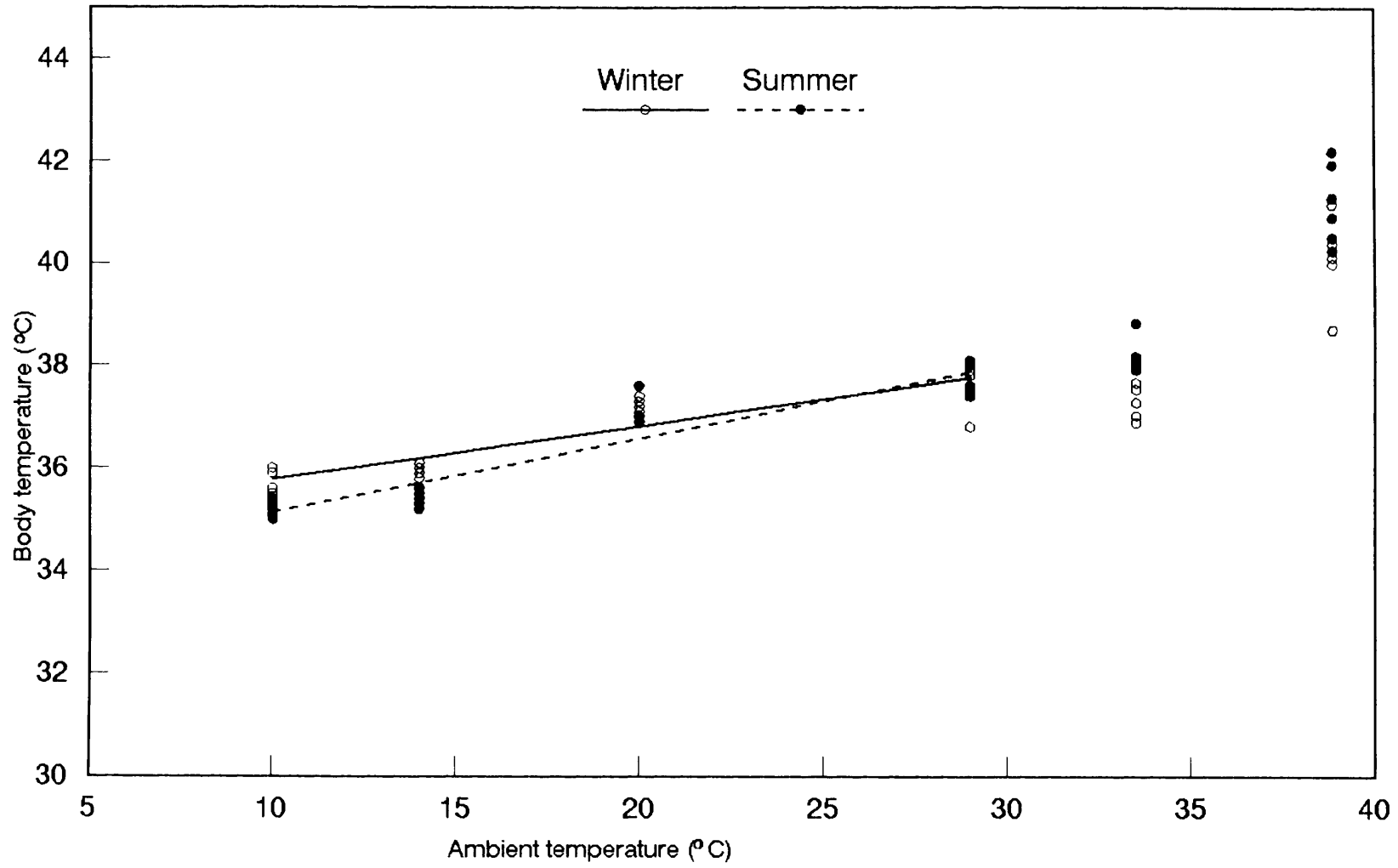
Fig. 14. Body temperature of summer and winter acclimatized X. inauris against ambient temperature.

Below thermoneutrality, C remained relatively constant with mean values that were not significantly different (t= -1,73; df=30; P<0,05) of 0,0653 $\pm$ 0,0049 and 0,0699 $\pm$ 0,0125 ml O_2/g/h/ °C for summer and winter animals respectively (Fig 13). As temperatures between 29 and 33° C were not intensively monitored a defnite minimal oxygen consumption could not be measured.

The length of dorsal and ventral body fur and tail hairs of summer acclimatized squirrels were significantly shorter than those of winter acclimatized squirrels (Table 16).

Table 16. Hair properties of X. inauris during the cold-dry (winter) and hot-wet (summer) seasons of the year.

Season	Dorsal fur (cm)	Ventral fur (cm)	Tail hairs (cm)
Winter n=10	6,19±0,30	9,24±0,26	42,10±1,28
Summer n=10	5,36±0,50	8,26±0,44	40,25±1,39
Student's t-test between seasons	t=-4,48; df=18 (P<0,001)	t=-5,99; df=18 (P<0,001)	t=-3,09; df=18; (P<0,001)

Ground squirrels remained calm at temperatures within the TNZ and below. Below T_a = 20° C piloerection was noted and the animals crouched in an upright position with tails tucked around their bodies. At T_a's greater than 33° C, the squirrels became progressively stressed as was clear from their more restless behaviour when not lying prone on the floor of the respirometer. Squirrels lay prostrate with legs extended and it was noted that they became moist on their ventral surfaces of the throat at T_a > 38° C, and breathed quick shallow breaths (polypnoea).

Table 17. Energy metabolism and thermoregulation in some rodents from arid environments.

SPECIES	MASS g	TNZ °C	T °C	VO₂ O₂/g/h		CONDUCTANCE O₂/g/h/°C	AUTHOR
Perognathus longimembris	8,9	30	35	1,07		0,280	Chew et al. 1967
Leggadina hermansburgensis	12,2	31 - 36	38	1,91	± 0,2	0,299	MacMillen et al. 1972
Gerbillus pusillus	12,6	32 - 38	35	1,05		0,240	Buffenstein et al, 1985
Perognathus intermedius	15,2	33 - 36	37	1,32		0,221	Bradley et al. 1975
Peromyscus eremias	20,0	30 - 37	36	1,32		0,190	McNab et al. 1963
Perognathus californicus	22,0	33	38	0,97		0,190	Tucker 1965
Gerbillurus nanus	28,4	33	39	0,78	± 0,1	0,146	Haim 1984
Gerbillurus paeba	31,1	33 - 36	37	0,89	± 0,2	0,310	Buffenstein 1984
Peromyscus truei	33,0	29 - 35	37	1,28		0,140	McNab et al. 1963
Notomys cervinus	34,0	33	--	1,22		0,190	MacMillen et al. 1972
Gerbillurus allenbyi	36,3	28 - 35	37	1,10	± 0,1	0,126	Haim 1984
Dipodomys merriami	38,0	32 - 35	37	1,13		0,110	Carpenter 1966
Acomys cahirinus	42,0	27 - 33	37	1,10	± 0,2	-----	Scholnik et al. 1969
Liomys salvani	44,0	31 - 34	37	1,07		0,190	Hudson et al. 1966
Aethomys namaquensis	48,4	32 - 34	36	0,89	± 0,1	0,160	Buffenstein 1984
Acomys russatus	51,1	30	37	0,80	± 0,3	-----	Scholnik et al. 1969
Eutamias minimus	53,4	30	36	0,98		-----	Willems et al. 1975
Dipodomys desertii	75,0	33 - 35	37	1,23		0,130	McNab 1979
Ammospermophilus leucurus	96,1	29 - 32	38	1,30		-----	Wang et al. 1971
Jaculus desertii	106,0	33 - 35	37	0,87		0,080	McNab 1979
Sigmodon hispidus	152,4	30 - 34	38	0,83		0,078	Scheck 1982
Spermophilus townsendi	163,8	31	36	0,67		-----	Hudson et al. 1972
Spermophilus tereticaudus	167,2	30	36	0,56		-----	Hudson et al. 1972
Neotoma fuscipes	187,0	---	37	0,80		0,059	Lee 1963
Paraxerus c. cepapi	223,6	34	39	0,65	± 0,1	0,071	Viljoen 1985
Spermophilus mohavensis	239,5	32	37	0,47		-----	Hudson et al. 1972
Spermophilus beldingi	253,3	32	37	0,69		-----	Hudson et al. 1972
Sciurus carolinenis	557,0	30	39	0,62	± 0,9	-----	Innes et al. 1979
Xerus inauris (winter)	559,9	28 - 32	38	0,70	± 0,1	0,069	Present study
(summer)	547,5	29 - 33	38	0,62	± 0,1	0,065	Present study

Table 18. Group sizes of <u>X. inauris</u> in the Kalahari Gemsbok National Park noted between 1985 and 1989. Sample size is in parentheses.

MONTH	1985	N	1986	N	1987	N	1988	N	1989	N
January	2,6 ± 1,5	(6)	-------		3,0 ± 1,1	(6)	-------		6,3 ± 1,6	(8)
March	2,0 ± 1,0	(7)	2,8 ± 1,5	(6)	-------		5,5 ± 3,3	(8)	5,3 ± 2,2	(8)
May	2,3 ± 0,9	(7)	3,6 ± 1,4	(11)	3,2 ± 0,8	(5)	-------		5,6 ± 2,2	(8)
July	2,3 ± 0,9	(7)	3,6 ± 2,2	(9)	6,2 ± 4,3	(13)	6,9 ± 2,8	(11)	-------	
Sept	2,5 ± 0,8	(6)	-------		3,8 ± 2,4	(8)	4,4 ± 2,6	(9)	5,3 ± 1,5	(8)
Dec	2,3 ± 1,0	(6)	3,3 ± 1,2	(3)	5,2 ± 4,5	(6)	4,2 ± 2,7	(10)	4,6 ± 1,2	(10)
Average (x)	2,3 ± 0.21		3,3 ± 0,38		3,6 ± 2,4		5,3 ± 1,24		5,4 ± 0,61	
Average rainfall mm/year	137,2		125,7		168,5		326,0		238,9	

Field observations revealed that during winter (cold-dry) squirrels emerged 1h 35 min (n = 13) after sunrise, significantly later than the 1h 10 min (n = 22) during summer (hot-dry and hot-wet periods) (t = 3,57; df = 33; P < 0,05). At the time of emergence the winter T_a's averaged 11,48 $\pm$ 3,1° C, while summer temperatures averaged 21,7 $\pm$ 3,6° C. In winter squirrels showed piloerection, huddling and extensive grooming in the sunlight at the burrow entrance for $\pm$ 1 h, while summer animals commenced foraging without delay (Chapter 4).

The parasol activity of the umbrella tail occurred from approximately two hours after sunrise and even in the shade during summer. The tail posture was characteristically arched-shaped and the animal orientated away from the sun. Shade foraging was preferred and by midday a siesta in nearby burrows or the central burrow system commenced, that continued until $\pm$ 16h00. During summer, the siestas were up to five h long and ambient temperatures averaged 32,9 $\pm$ 3,8° C during the period. Shorter siesta periods of 3 h 30 min commenced when the ambient temperature reached 22,9 $\pm$ 2,3° C. The total above ground time did not differ significantly between seasons and measured on average 6 h 31 min , 6 h 18 min and 6 h 25 min for winter (n = 13; cold-dry), summer (n = 12; hot-dry) and summer (n = 10; hot-wet) respectively. During the summer periods, when soil temperatures of up to 65° C were measured at 16h00 in the afternoon, squirrels would forage for short spurts and go underground, presumably to offload their accumulated heat. These short retreat bouts would continue until $\pm$ 17h30, when the soil surface cooled to below 45° C. Sandbathing occurred frequently during summer and was also observed on warmer winter days. On rainy, windy and very cold days, squirrels would spend very little time outside their burrows (Chapter 4).

Table 19. Body temperatures (T$_b$) of winter acclimatized *X. inauris* when groups of 2, 4 and 6 animals at T$_a$ from 14° C to 29° C. T$_b$ without or with nesting material are significant at P<0,05(*), using the t-statistic.

	No nesting material			With nesting material			
T$_a$ ° C	Group size (N)	Sample size (n)	T$_b$ ° C	Group size (N)	Sample size (n)	T$_b$ ° C	Without/with nesting material F test
29	2	6	37,6 ± 0,02	2	4	37,6 ± 0,03	F = 0,4; P=0,087
	4	6	37,5 ± 0,32	4	4	37,9 ± 0,23	F = 12,0; P=0,174
	6	6	37,8 ± 0,50	6	4	38,1 ± 0,25	F = 6,7; P=0,214
22	2	-		2	-		
	4	4	37,2 ± 0,17	4	4	37,5 ± 0,18	F = 20,2;*P=0,004
	6	-		6	-		
20	2	6	37,0 ± 0,15	2	4	37,2 ± 0,15	F = 48,9;*P=0,004
	4	6	36,4 ± 0,15	4	4	37,1 ± 0,16	F = 84,3;*P=0,000
	6	6	37,4 ± 0,04	6	4	37,4 ± 0,18	F = 2,9; P=0,143
16	2	-		2	-		
	4	4	36,3 ± 0,18	4	4	36,5 ± 0,12	F = 19,2;*P=0,055
	6	-		6	-		
14	2	4	35,9 ± 0,10	2	4	36,1 ± 0,09	F = 16,7;*P=0,006
	4	4	36,0 ± 0,15	4	4	36,5 ± 0,04	F = 21,0;*P=0,008
	6	4	36,2 ± 0,04	6	4	36,5 ± 0,04	F = 71,3;*P=0,000

Thermoregulation in huddled squirrels

In the free-living squirrels group sizes correlated significantly with rainfall (y = 1,3 + - 0,01x; r=0,74; n=8; P<0,05). Between 1984 and 1987, the southern Kalahari experienced a severe drought. Since 1988 however, rainfall has increased. Lumping the drought years data on group size, and comparing these with the wet years, a significant increase in numbers was found in the post-drought years (t=-4,69; df=22; P< 0,001) (Table 18).

Mean daily temperatures of the burrow at depths of 400 and 800 mm during summer were constant at 29,9 $\pm$ 1,5° C and 30,6 $\pm$ 0,1° C respectively (Fig. 3, Chapter 3). Burrow temperatures never exceeded 31,0° C in summer. Mean daily burrow winter temperatures were less constant and varied between 10,3 $\pm$ 1,7° C at 40 cm and 15,1 $\pm$ 0,9° C at 80 cm. Lowest temperatures in the burrows during winter never declined below 7,0° C (Fig. 4, Chapter 3). An average of 80 $\pm$ 10 min (n = 13) of huddling and basking occurred at the entrance of the central burrow system during winter, with shorter socializing periods of 20 min during the summer seasons (Chapter 4).

In the laboratory body temperatures of squirrels given no nesting material were significantly lower than squirrels with nesting material, irrespective of group size, when tested at ambient temperatures of 14, 16, and 22° C, but not at 29° C (Table 19).

The VO_2 consumption of squirrels given no nesting material was significantly higher than those provided with nesting material (Table 20). The average percentage difference at T_a's 14, 20 and 29° C were 4,9 %, 4,2 % and 2,4 % respectively for groups with or without nesting material.

Conductance was found not to differ significantly between squirrels tested with or without nesting material. Conductance was significantly higher for groups of squirrels without nesting material than with it at most T_a's. The only exception was for squirrels tested at 20° C huddled in groups of four and two and squirrels tested at 29° C huddled in groups of two, four or six (Table 20).

Both the VO_2 and C decreased significantly (t-test) with an increase in huddled group sizes at all T_a's, except in the case of C between group sizes of two and four at T_a =20 ° C (Tables 20 and 21). Neither of these parameters differed when group size was changed and tested at T_a of 29° C (Table 20). The largest energy savings per g squirrel mass of 42,7 % and 40,0 % were measured for C

Table 20. Thermoregulatory measurements of huddled Cape ground squirrels. VO_2 = Oxygen consumption; C = conductance. Differences between VO_2 and conductance with and without nesting material in rows were significantly different at $P<0,05$ (t-test)(*).

T_a °C	N	No nesting material VO_2	C	With nesting material VO_2	C
29	6	0,675 ± 0,006*	0,077 ± 0,001NS	0,698 ± 0,006	0,075 ± 0,002
	4	0,653 ± 0,002*	0,076 ± 0,012NS	0,640 ± 0,004	0,072 ± 0,001
	2	0,619 ± 0,010*	0,072 ± 0,001NS	0,601 ± 0,003	0,069 ± 0,002
22	4	0,914 ± 0,010*	0,060 ± 0,001*	0,891 ± 0,003	0,058 ± 0,001
20	6	0,800 ± 0,001*	0,048 ± 0,002*	0,749 ± 0,008	0,045 ± 0,002
	4	0,954 ± 0,005*	0,058 ± 0,001NS	0,916 ± 0,012	0,058 ± 0,012
	2	0,994 ± 0,006*	0,058 ± 0,000NS	0,972 ± 0,003	0,057 ± 0,000
16	4	1,278 ± 0,019*	0,063 ± 0,001*	1,126 ± 0,025	0,055 ± 0,001
14	6	0,983 ± 0,006*	0,044 ± 0,001*	0,928 ± 0,003	0,041 ± 0,000
	4	1,356 ± 0,019*	0,061 ± 0,001*	1,314 ± 0,009	0,059 ± 0,001
	2	1,491 ± 0,006*	0,068 ± 0,001*	1,401 ± 0,007	0,063 ± 0,000

Table 21. Percentage energy saving of VO_2 = oxygen consumption and C = conductance for X.inauris in groups of 1, 2, 4 and 6 tested at ambient temperatures (T_a) of 14 and 20° C. Significance ** = P<0,001 or not significant = NS. Df=8,0.

T_a	Group	vs	group	% Energy saving	Metabolic variable	Student t-test
				WITHOUT NESTING MATERIAL		
14	6		1	42,67	C	20,07; df=8,0**
				40,00	V	18,39; df=8,0 **
	6		2	35,19	C	-9,78; df=6,0 **
				34,09	V	11,50; df=6,0 **
	4		1	18,23	C	15,62; df=8,0 **
				17,23	V	18,25; df=8,0 **
	2		1	8,58	C	12,31; df=8,0 **
				8,97	V	12,69; df=8,0 **
20	6		1	36,29	C	7,17; df=8,0 **
				38,78	V	7,67; df=8,0 **
	6		2	17,64	C	13,09; df=6,0 **
				19,51	V	12,75; df=8,0 **
	4		1	23,04	C	4,58; df=8,0 **
				27,04	V	8,31; df=8,0 **
	2		1	29,28	C	4,49; df=8,0 **
				23,94	V	4,73; df=8,0 **
				WITH NESTING MATERIAL		
14	6		2	34,60	C	-9,75; df=6,0 **
				33,00	V	11,50; df=6,0 **
	4		2	6,64	C	17,84; df=6,0 **
				6,21	V	13,33; df=6,0 **
20	6		2	20,80	C	13,09; df=6,0 **
				23,00	V	19,75; df=6,0 **
	4		2	1,57	C	-1,17; df=6,0 NS
				5,77	V	10,35; df=6,0 **

and VO_2 in groups of 6 against 1 at T_a of 14 °C, followed by 36,3 and 38,9 % saving for C and VO_2 respectively for groups of 6 versus 1 measured at T_a of 20 °C (Table 21).

The EWL of grouped squirrels tested below the TNZ decreased with a decline in T_a and group size. The EWL for squirrel groups of two was significantly higher than for groups of 4 or 6 (at T_a 14 and 20 °C).

The EWL results showed that all group sizes at T_a's 14 and 10° C with nesting material has higher EWL than animals without nesting material. However at 29 °C the converse was true as indicated by the t-tests in Table 22.

Table 22. Evaporative water loss (EWL) (mg H_2O/ g / h) of
         X. inauris at ambient temperatures between 14 to 29 °C. N=group sizes.

T_a° C	N	No nesting material EWL	With nesting material EWL	t-values
29	6	1,5106 ± 0,008	1,5661 ± 0,014	6,98; df=6,00; P< 0,001
	4	1,2540 ± 0,040	1,3980 ± 0,021	6,19; df=6,00; P< 0,001
	2	0,6149 ± 0,008	0,6284 ± 0,032	2,45; df=6,00; P< 0,001
20	6	0,1602 ± 0,008	0,1566 ± 0,004	-3,23; df=6,00; P< 0,001
	4	0,1679 ± 0,016	0,1640 ± 0,005	6,92; df=6,00; P< 0,001
	2	0,1738 ± 0,002	0,1713 ± 0,003	2,92; df=6,00; P< 0,001
14	6	0,1341 ± 0,001	0,1312 ± 0,009	-3,67; df=6,00; P< 0,001
	4	0,1415 ± 0,001	0,1385 ± 0,002	5,39; df=6,00; P< 0,001
	2	0,1447 ± 0,001	0,1225 ± 0,001	3,06; df=6,00; P< 0,001

At 14 and 20° C, the grouped squirrels without nesting material had significantly higher EWL than squirrels with nesting material. The opposite was true when tested at T_a of 29 °C and EWL increased when nesting material was added (Table 22).

DISCUSSION

Single squirrels

As T_a's increase, animals are faced with the potential problem of excess heat gain from the environment. The classical view of endothermy is that T_b is to remain constant within the thermoneutral zone, increasing when the T_a rises above the upper critical temperature as regulatory processes become ineffective (Folk 1974). An increase constitutes hyperthermia, which is advantageous for animals with sensitive thermal inertias and where precise regulation of T_b would entail extravagant expenditure of vital energy and water supplies. Evidence from other desert rodents exposed to high ambient temperatures shows that most of them solve this largely by a tolerance of hyperthermia (MacMillen & Lee 1970, Wunder 1975, Chappell & Bartholomew 1981, Yousef 1980, Buffenstein & Jarvis 1985b, Du Plessis, Erasmus & Kerley 1989).

Like other large diurnal squirrels such as Spermophilus leucurus and Citellus leucurus (Hudson 1962) both summer and winter acclimatized X. inauris elevated their T_b's up to a maximum of 43° C in the face of T_a's above the thermoneutral zone. But the summer acclimatized animals allowed their T_b's to rise significantly higher than the winter acclimatized animals, as found in other rodents (Yousef 1980). In X. inauris, T_b increased within the TNZ while VO_2 remained constant, which led to substantial heat storage. The hyperthermia experienced at higher T_a's would enhance the animals' water economy and ability to stay longer out during the day at higher T_a's. Salivation only occurred in the laboratory when animals were exposed to T_a's above 40° C as noted for C. leucurus (Hudson 1964), but in the wild such temperatures would be avoided by taking refuge into their burrows.

There are limitations to the T_b at which a mammal can remain active as the upper lethal T_b's range between 42° C - 43° C (Schmidt-Nielsen 1964). The broader generalized spectrum of T_b's for small mammals above the TNZ is between 34° C - 42° C (Morhardt & Gates 1974). X. inauris were able to fluctuate their T_b's and this could be advantageous to them living in transient states of energy imbalance during unpredictable arid climatic changes. Like the sand rat, P. obesus (Ilan & Yom-Tov 1990), X. inauris also made use of siestas during both summer and winter, related to the annual pattern of daily temperature distribution (Fig. 2 & 3; Chapter 2). X. inauris peak activity preceded the hot hours of the day and peaked again when T_a declined in the late afternoon in summer. They remained in their burrows on average for 18 h daily (Fig. 6, Chapter 4). This is in contrast to other ground squirrels (Spermophilus spp.) which remained active during the hottest and coldest periods of the day (Hudson 1964). X. inauris off-loaded body heat between foraging bouts in the late afternoon in summer by returning underground, as found to occur in Abert's squirrels (Sciurus aberti) (Golightly & Ohmart 1978). Sandbathing, a way of dissipating heat, recorded in antelope ground squirrels (Chappell & Bartholomew 1981) and prairie dogs (Reinking, Delbert & Fairbanks 1978) was frequently practised by X. inauris. Squirrels also lay flat on their bellies in the shade with their legs outstretched, and simultaneously scratching the sand surface layers away to reach cooler sand underneath, another means of off-loading body heat.

Furthermore, excessive heat loading was avoided by using the tail as a parasol (Van Heerden & Dauth 1987), also noted for Abert's squirrel (Golightly & Ohmart 1978). The tail is dorsoventrally flattened above the body, and is held in this position whenever the intense solar radiation is at its greatest. With the tail raised and their backs orientated towards the sun, T_b was estimated to be reduced by over 5° C, which, in turn allowed extended periods of foraging (Bennett et al. 1984). Salivation is regarded as an emergency measure when body temperatures reached lethal levels of 43° C (Schmidt-Nielsen 1964), but

has never been observed in the wild as free-ranging animals avoid such extreme temperatures behaviourally.

The pelage forming a short glossy external protective layer is a reflective shield to radiation in summer and through pilo-erection facilitating heat retention during the cold. In addition, the colour of X. inauris pelage, apart from the main function of crypticity, is also associated with its thermal biology. Furthermore the so-called hypothesis of 'maxithermy' can explain the possible advantages of X. inauris having a black skin. Hamilton (1975) explained that a black skin can only be of advantage to the animal, enabling it to raise its body temperature rapidly during heat exposure. In X. inauris this phenomenon plus being able to withstand hyperthermia could ensure the continuation of other essential life processes such as feeding, digestion and reproduction in the face of higher than TNZ ambient temperatures. Similar results were found for Bedouin goats (Capra hircus) having a black skin and black hair (Finch, Dmi'el, Boxman, Shkolnik & Taylor 1980). This interesting aspect of X. inauris thermoregulatory abilities needs further investigation.

At T_a's of less than $20°$ C, X. inauris lowered their T_b but, in all cases, winter acclimatized animals maintained slightly higher T_b's than summer acclimatized animals. This probably resulted from cold adaptation with longer fur, lower conductances and a higher RMR.

Scholander (1955) pointed out that it is not possible to increase the fat insulation of small mammals markedly, they therefore increase hair length in winter. X. inauris in growing their ventral and dorsal fur, decreased winter conductances. This phenomenon, plus increased thermogenic capacity in association with assimilation of enough energy from their environment, removed the need to become hypothermic. Haim et al. (1987), found that X. inauris responded to nor-adrenaline injections, increasing VO_2 and T_b. This indicated that non-shivering thermogenesis, which is associated with brown fat, can occur. This process is advantageous to squirrels and small mammals in general as heat

is generated without the involvement of muscle contraction (Jansky 1973, Heldmaier 1975). Behavioural means of gaining extrinsic heat, such as basking in the sun, are also advantageous as these reduce the need to metabolize reserves. Alkon, Degen, Cohen & Pollak (1986) observed porcupines basking in the sun on winter mornings. Furthermore, the solar heat gain of rock squirrels (S. variegatus) at low wind speeds was about 20 % greater in winter coats than in summer coats (Walsberg & Schmidt 1989). On cold days (average $\pm$ 12-15 ° C) X. inauris foraged preferentially in the sun with their fur fluffed.

Haim et al. (1987) found that his acclimated X. inauris measured up to 20 % lower than the BMR values than predicted by Brody (1945). X. inauris's lower than predicted metabolism was as expected for a desert dwelling rodent (McNab 1963, Bradley et al. 1975). The higher metabolic rate of winter acclimatized squirrels possibly permits the tolerance of lower environmental and burrow temperatures. These metabolic results were likely to be a consequence of prevailing high conductances. Whilst without reduced conductances, the lowering of metabolism was impossible, as was suggested in the study of two other arid-adapted rodents Thallomys paedulcus and Aethomys namaquensis (Lovegrove, Heldmaier & Knight in press).

Because small mammals have larger surface to volume ratios than large mammals, conductance is inversely related to body size (Scholander 1955, Sealander 1964, Aschoff 1981). Conduction is also the reciprocal of insulation (Scholander, Hock, Walters & Irving 1950). Hudson, Deavers & Bradley (1972) reported C values of several species of ground squirrels that were generally slightly higher than the predicted values. Using the C equation for sciurids from Bradley & Deavers (1980), summer and winter acclimatized had C values of 23,2 and 29,9 % higher than the estimated prediction, indicating lower insulative values of the pelage. Heat could be lost over a relatively small surface/volume ratio. However winter animals had longer fur and relatively lower C's. T_b's declined, but only to a minimum of 35° C. At a T_a of 10° C, the metabolic rate increased three-fold above the minimal level, but C remained

relatively constant, suggesting that C played a minor part in thermoregulation. This is true for many small mammals (Bradley & Deavers 1980, Buffenstein & Jarvis 1985 a & b).

Grouped squirrels

Although X. inauris groups in the southern Kalahari are generally small in size varying between three and 11 individuals, large group sizes have been reported in Botswana (Smithers 1983). Rainfall correlated positively with squirrel group size and was indirectly affected by the balance between preferred habitat and food supplies (Table 18). Prairie dog (C. ludovicianus) coteries ranged between 5 to 8 individuals in dry areas of south Dakota. These group sizes were also affected by rainfall (King 1955).

Burrow systems provide thermally stable microhabitats for X. inauris for most hours of the day. Burrow temperatures are actually the equilibrium value between the burrow air and surrounding soil. Irrespective of whether the outside temperatures fluctuated between 15,0 to 17,0 ° C over a 24 h period during winter, the burrow temperatures only varied, between 9-10 ° C (Fig. 3 and Fig. 4, Chapter 3). A single squirrel would encounter thermoregulatory difficulties during sub-zero ambient temperatures above and below ground during winter mornings and nights. This problem is circumvented by group living and through huddling. Although the burrows cooled, sometimes to as low as 7° C, the decline was buffered by soil depth, declining more slowly than the above ground ambient temperature. It therefore provides one explanation (apart from other social and physiological pressures) for squirrels being colonial and living in coteries in burrow systems. Huddling has been shown to reduce the metabolic cost of thermoregulation for mammals and birds (Sealander 1952, Pearson 1960, Mount 1960, Baudinette 1972, Glasser & Lustick 1975, Pinshow, Battles & Schmidt-Nielsen 1976, Withers & Jarvis 1980, Karasov 1983b). This phenomenon is also apparent in reptiles (White &

Table 23. Oxygen consumption of huddled groups of rodents.

SPECIES	MASS g	Ta °C	VO_2 ml O_2/g/h				AUTHOR
			single(no fur)	single(no nest)	3 mice(nest)		
R. megalotis	8	20	0,82	0,60	0,50		Pearson
		30	0,45	0,40	----		1960
			single(nest)	single(no nest)	3 mice(no nest)	3 mice(no nest)	
Peromyscus	25	7	2,7 ± 0,3	3,0 ± 0,4	2,0 ± 0,4	6,0 ± 0,5	Vogt et al.
		13	1,7 ± 0,2	4,4 ± 0,2	1,8 ± 0,1	3,2 ± 0,4	1982
			single(no nest)	2 (no nest)	4 (no nest)		
Heterocephalus	40	15	2,5 ± 0,1	1,7 ± 0,1	1,5 ± 0,2		Withers et al.
		25	2,1 ± 0,1	2,0 ± 0,2	0,5 ± 0,1		1980
Ammospermophilus			single(no nest)	5 (nest)			
	100	10	3,1 ± 0,1	1,1 ± 0,1			Karasov
			single(no nest)	5 (no nest)			1983
		15	2,9 ± 0,2	1,9 ± 0,1			
			2 (no nest)	6 (no nest)	2 (nest)	6 (nest)	
Xerus inauris	560	29	0,6 ± 0,0	0,7 ± 0,0	0,5 ± 0,0	0,7 ± 0,0	Present
		20	1,0 ± 0,0	0,8 ± 0,0	0,9 ± 0,0	0,7 ± 0,0	study
		14	1,5 ± 0,0	1,0 ± 0,0	1,4 ± 0,0	0,9 ± 0,0	

Lasiewski 1971) and insects (Nagy & Stallone 1976). The body temperatures of single X. inauris without nesting material, varied up to 2° C when tested at ambient temperatures of 29 to 14° C. However, when squirrels were placed in groups of two, four and six, the T_b variation declined to between 1,7, 1,5 and 1,4° C respectively. This declined as a hypothermic tendency was also found to occur in naked molerats (Withers & Jarvis 1980) but not in neonatal pigs (Sus scrofa) when huddled together in groups (Mount 1960) (Table 23).

Temperatures encountered by X. inauris below the lower critical temperature in any habitat or season would require energy production greater than the RMR level, but when huddling was employed, temperatures below the TNZ were not much of an energetic burden. Whether or not energy requirements for most winter-active endotherms actually increase during the cold-dry winter months is not clear. However, single winter acclimatized squirrels did show a significant increase in their VO_2 consumption. Huddled winter acclimatized squirrels in contrast showed lower marked increments of heat production when T_a declined than did single squirrels. At 14° C, without providing nesting material, when single animals showed signs of shivering thermogenesis, groups of two, four and six squirrels could save between 9,0 % and 40,0 % of their energy expenditure respectively. Thermoregulation was therefore achieved at a 1,6 fold lower energy cost when 4 or 6 squirrels huddled than the costs to a single squirrel at 20 and 14° C. As expected, single winter acclimatized squirrels showed an increase in metabolism and it can therefore be concluded that, through huddling, potentially more energy could be saved without an increase in metabolism. In order for the huddling alternative to be a success, good group cohesion is required. The improved insulation and relatively smaller surface area of the huddled groups functioned as predicted by the Kleiber metabolic rate versus body size rule (Kleiber 1975). The effects of huddling were further enhanced with the addition of nesting material. At a T_a of 20° C, the energetic saving of 6 squirrels without nesting material against two was 19,5 % lower than a similar experiment where nesting material was added and resulted in a

23,0 % saving. These differences were significant. The effect of the artificial nesting material (possibly similar to the grass found in natural nests) brought about a 4,0 % energy saving, which is remarkable, although not much in the light of the so-called overall thermal problem.

Close proximity retarded heat loss in roosting pallid bats (<u>Antrozous pallidus</u>) and decreased their individual metabolic rates (Trune & Slobodchikoff 1976). <u>Microtus agrestis</u> showed reduced metabolism from 10-20 % as a result of the heat economy of huddling when four to eight voles were grouped together (Hansson & Grodzinski 1970). Likewise huddling behaviour in <u>Peromyscus leucopus</u> decreased energy expenditure by 16-33 % (Vogt & Lynch 1982) (Table 23). Karasov (1983b) found a 64,0 % decrease in nocturnal energy expenditure for <u>A. leucurus</u> when allowed to huddle in a nest and <u>Microtus arvalis</u> reduced its daily metabolic rate by 43,0 % when clumped in a group (Grodzinski, Makomaska, Terth & Weinter 1977).

Providing a nest for a group of seven <u>P. leucopus</u> permitted an 18-28% energy saving (Vogt & Lynch 1982). Winter acclimatized <u>Tamiasciurus hudsonicus</u>, saved 18 % energy by huddling in a nest instead of huddling without a nest (Pauls 1981). The effect of the nest under natural conditions, the possible manipulation of it and the postural adjustments as well as the effect of the underground tunnel system and its warmer conditions may be of greater value to <u>X. inauris</u> than could be measured in the laboratory.

Group conductance was not stable as was the case for single squirrels but rather declined with decreasing T_a as a consequence of group size and slightly lowered T_b. Red squirrels (<u>T. hudsonicus</u>) showed a seasonal change in conductance and lowered their conductance by 60,0 % during winter when provided with a nest (Pauls 1981). The similarity of T_b for individual and huddled squirrels, but the marked differences in VO_2, indicated noncomparable values for conductance. Since conductance is measured indirectly from VO_2, T_b and body mass can be

non-uniform and as so many variables play a role, the results therefore must be treated with caution (McNab 1980).

Comparative data available for rates of pulmocutaneous water loss of desert rodents made in thermal neutrality have been summarized by MacMillen (1972). X. inauris results compare favourably with other rodents (MacMillen 1972, Baudinette 1972). The lowered VO_2 and smaller exposed surface area (per individual) of larger huddled groups of squirrels resulted in the decrease in group EWL. Naked molerats (Withers & Jarvis 1980) and Australian hopping mice (Baudinette 1972) lowered EWL when huddling. The reduction of EWL can also be an adaptive phenomenon in response to limited water supply during the dry and cold winter months (Hinds & MacMillen 1985). Huddling may only have an effect on water balance if the relative humidities of the burrows are not high and saturated as is the case for mole-rats (Withers & Jarvis 1980). The overall EWL measured for huddled squirrels at T_a 29° C probably also reflected the magnitude of respiratory water recovery and the effectiveness of the counter-current heat exchange system characteristic of rodents (Jackson & Schmidt-Nielsen 1964). Caution should be exercised when measuring EWL in general, as Buffenstein & Jarvis (1985b) reported that experimental technique and specifically the influence of chamber humidity can result in incorrect measurements.

Summary

The combination of large body size, huddling and metabolic attributes such as heat dissipating capacities during the hot summer, were of great energetic saving value. Squirrels escape thermal extremes by some adaptive behavioural features such as burrowing, sandbathing, posture, usage of a parasol tail and huddling. It can be concluded that in X. inauris, behavioural responses to environmental temperature stimuli (using microclimatic burrows, nesting material huddling) were so efficient that insulative and physiological adaptations to macro-environmental temperatures were much reduced in

importance. Why are these rodents restricted to semi-arid areas and not found in in the more arid desert areas? Invasion of arid environments would only be possible on the periphery when favourable conditions prevail, such as above average rainfall, and enough growth of green soft forbs. The lack of sufficient quantity and quality of foods can be a disadvantage for X. inauris of large body size.

CHAPTER 6

ASPECTS OF DIGESTION AND MORPHOLOGY OF THE DIGESTIVE TRACT

INTRODUCTION

Theoretically it has been suggested that possible changes from omnivory (Landry 1970) or granivory/insectivory (Vorontsov 1962) in mammals to herbivory, have been associated with climatic and vegetation changes during the Miocene (drier period) (Moir 1968). This may have facilitated several anatomical, physiological and behavioural adaptations (Vorontsov 1962), including the sacculation of animal stomachs. There is evidence of change from a primitive monogastric to an advanced digastric stomach with a papillated keratinized region and reduced glandular antrum in certain rodents (Carleton 1973, Langer 1986, Perrin & Curtis 1980) associated with the climatic changes of the Miocene.

Animals have to eat to stay alive, nutritional requirements being universal in terms of energy sources, carbohydrates, proteins, lipids and trace elements, and at the same time also being diverse, considering the different foods available and feeding mechanisms and digestive tract functions (Madge 1975). The efficiency of digestion of food by an animal represents a compromise between two competing factors, the rate of nutrient extraction and the rate of passage of food through the gut (Van Soest 1982). This relationship seems to have been very important in determining the food choice of large rodents (Van Jaarsveld 1983, Knight & Knight-Eloff 1987). Moreover, comparative gross morphological studies of muroid digestive systems have indicated a great diversity of stomachs and caeca (Vorontsov 1962, Carleton 1973, Snipes 1981). Recently gastro-intestinal studies of African rodents such as the Cricetidae and Muridae have demonstrated remarkable structural variations and some unusual adaptations

(Maddock & Perrin 1981, Perrin & Curtis 1980, Van Jaarsveld & Knight-Eloff 1984, Perrin 1986, Knight & Knight-Eloff 1987, Forman & Phillips 1988). In contrast, the gut morphometrics of the Sciuridae have been poorly studied. Antelope ground squirrels (A. leucurus) take food from diverse sources when no free-standing water is available. Their digestion requires high levels of dietary protein (Karasov 1982) and a major diet switch occurs when the seasons change (Karasov 1985). It was suggested that their gut flora must be quite adaptable but no mention was made of gut morphology nor whether they make use of coprophagy. A study on several species of tree squirrels in Africa by Rahm (1972) indicated that frugivores had relatively longer small intestines and colons, in constast to insectivorous species. However, Viljoen (1980), found that tree squirrels of the genus P. cepapi, had relatively short small intestines and colons in comparison with the other African tree squirrels, but that they are frugivores and not insectivores as predicted by Rahm, questioning the validity of Rahms' postulation.

Efficient digestive processes in conjunction with a longer large intestine, which is typical of arid-adapted species, and the possible use of coprophagy would be important to a small herbivore such as X. inauris with its relatively high mass-specific energy requirements. The functional importance of a caecum, as in other rodents and small mammals, for the digestion, fermentation and absorption of various food substances has been emphasized by Snipes (1979; 1981; 1982) and Knight & Knight-Eloff (1987). X. inauris has a very distinct large caecum. However, apart from a description of the Xerus alimentary canal by Mitchell (1905), and the records on the skull and dentition by De Graaff (1981), very little is known about the morphology of the X. inauris digestive tract.

Since X. inauris may be classified primarily as a terrestrial hindgut-fermenter (Langer 1986), eating fresh leaves, flowers, bulbs and tubers, with insect remains appearing in trace quantities (Herzig-Straschil 1979) (Chapter 3), it might be expected that the digestive tract would include an elaborate stomach,

capacious caecum and relatively long large intestine. Furthermore, the fact that X. inauris conserve it's water flux, producing concentrated urine and dry faeces when deprived of water (Chapter 7), gives rise to the hypothesis that the fluid absorption and fibre digestion in the large intestine, i.e. caecum and colon, could possibly play a very important role during adverse conditions. The purpose of the present study was to examine these assumptions, describe the morphology and histology of the digestive tract and also to measure transit time of digesta during different times of the year.

METHODS

Digestive system and morphology

Specimens were trapped in the field during December 1988. Fresh specimens were immediately processed. Body mass and standard body measurements were taken. The pH of the different gut regions was measured with a portable Digital Data Systems 800 pH/Mv meter, as was the pH of the cardiac and pyloric regions of the stomach, by inserting the electrode of the meter through a small slit in each region. Gut mass was determined with the parts of the tract still filled with digesta. The approximate zonations of the squamous and cuboidal glandular areas of the stomach were mapped using a binocular dissection microscope. The dimensions of the stomach and approximate surface areas of the glandular and non-glandular stomach regions were determined from outline tracings of the flattened stomach half-sections. The lengths and diameter of the hindgut sections, the small and large intestine and caecum, were measured to the nearest millimetre. Maximum gut volumes were determined through volumetric measurements using water.

For light microscopy, gut sections were fixed in acetic formaldehyde (AFA) or Bouin's fluid, and stored in 70 % alcohol. Following routine embedding, sections were cut at 7 μm, stained with Ehrlich's haematoxylin and counter-stained with eosin and Masson's trichrome (Humason 1962). A minimum of five thickness measurements for each layer of the gut wall were determined with the aid of a micrometer. Specimens were taken from several areas in the antrum and corpus of the stomach, two from the duodenum, ileum and jejenum, one each from the apex ceci, proximal colon and the distal colon. Digesta from the different tract parts were studied microscopically, to determine whether any bacteria or protozoa were present. Light micrographs were taken using a Carl Zeiss photomicroscope II.

Where more than two samples were measured, results are presented as means with standard deviations. Differences between means were initially tested using analysis of variance (F-test) (Cass 1973). Cass (1973) and Siegel (1956) were consulted for parametric and non-parametric tests, respectively.

Transit time of digesta

The rate of passage was determined using plastic pieces (2 x 2 mm) (Van Soest, Uden & Wrick 1983) feeding six squirrels at a time on separate occasions, during the summers of January 1987 and January 1990 as well as during the winters of June 1987 and August 1988. The rate of passage was determined following the thermoregulatory experiments. Prior to the digestive trials, they were starved for 24 h, and then presented with a rodent diet (Cerebos Food Corp. Ltd., Wadeville) (Refer to Chapter 7 for nutrient analysis of food) containing the marker food for four hours. After feeding, the faecal collection trays were inspected every hour for the next 80 h, until no more markers were found in the faeces.

RESULTS

Macroscopic   morphology

The narrow oesophagus extending from the mouth to the stomach, is 35,0 $\pm$ 2,0 mm in length and enters the stomach in the non-glandular   corpus ventriculi (Fig. 15 and 16). The stomach is oval-shaped, uni-locular, hemi-glandular and divided into two major compartments roughly equal in size. The non-glandular corpus is separated from the glandular antrum region by teeth-like fimbria or Grenzfalten. Food taken in and stored in the corpus has a green appearance at a pH of 4,8 $\pm$ 0,7 (Fig. 17) since gastric secretions have not yet acted on the plant-cell walls. However in the gastric region, where digestion has begun, the plant cells have lost their chloroplasts. Stomach contents have a pH of as low as 2,1 $\pm$ 0,5, significantly lower (t= 7,23; df = 14; P<0,001) than in the non-glandular corpus (Fig. 17). Food material is yellow-brown in colour and watery when passing from the pylorus into the small intestine. A distinctive feature of the corporal epithelium is the presence of filliform papillae projecting into the lumen. The glandular antrum could be subdivided into the fundus, cardiac and pyloric regions, with short transition areas between each. The shallow incisura angularis is found between the antrum and corpus of the stomach (Fig. 16).

The small intestine is an extensive, long, coiled tube lying between the pyloric and ileocaecal sphincters, with a mean length of 805,0 $\pm$ 127,0 mm and a diameter of 5,0 $\pm$ 1,5 mm. This was significantly (t=6,01; df = 14; P<0,001) longer than the large intestine (Table 24). As in most other mammals, the small intestine could be divided into a large duodenal loop, jejenum and ileum (also called the Meckel's tract) (Mitchell 1905). The jejenum could not be distinguished morphologically from the ileum, but the ileum is presumed to be the last loop leading into the caecum and is a quarter of the length of the whole intestine (Banks 1986). The small intestine had an average pH of 6,4 $\pm$ 0,4 which was not significantly lower than the pH found in the caecum (t = 1,22; df = 14).

C = corpus
PG = proper gastric
SI = small intestine
AC = apex ceci
ac = ampulla ceci
PC = proximal colon
CR = colon-rectum

1,5 cm
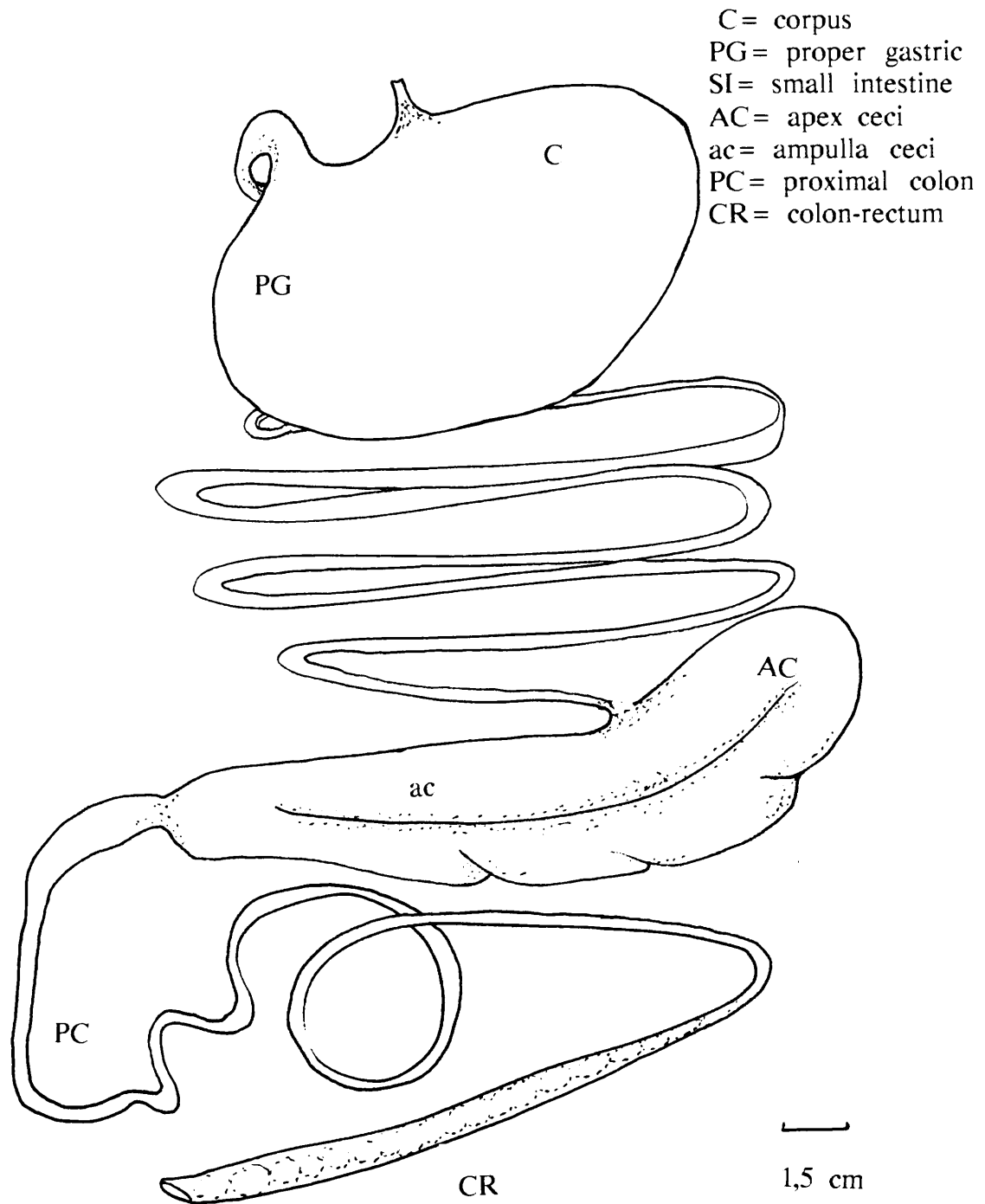
Fig. 15. Schematic drawing of the gastrointestinal tract of X. inauris.

Fv = fornix ventricularis
Cp = corpus ventriculi
Fu = fundus
Co = glandular corpus
Py = pyloric region
G = grenzfalte

1 cm
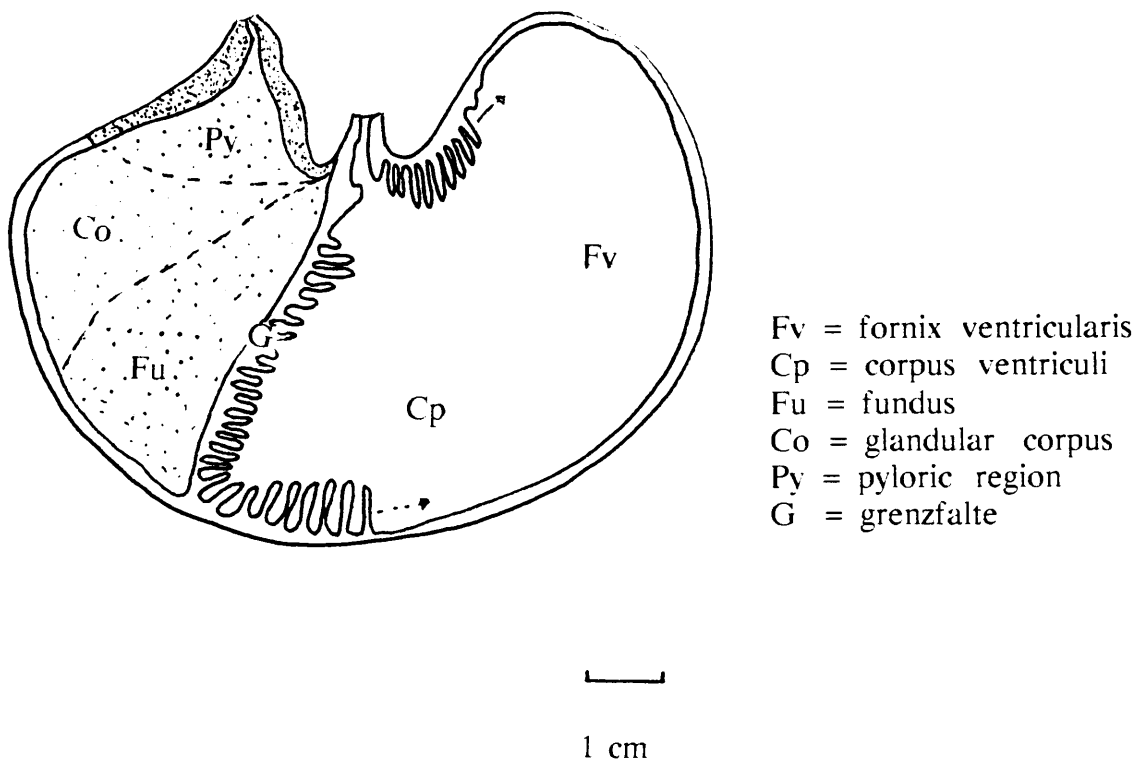
Fig. 16. Schematic view of the bisected stomach of X. inauris.
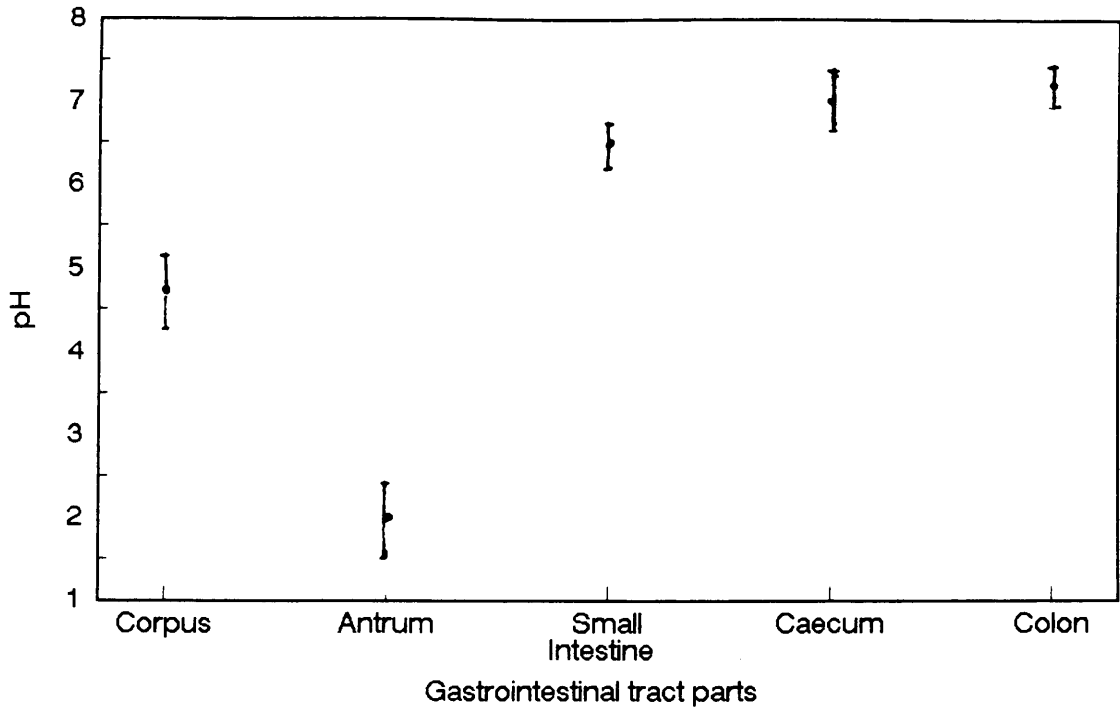
Fig. 17. Mean (+SD) pH values of the different gastrointestinal tract
parts. N=8.
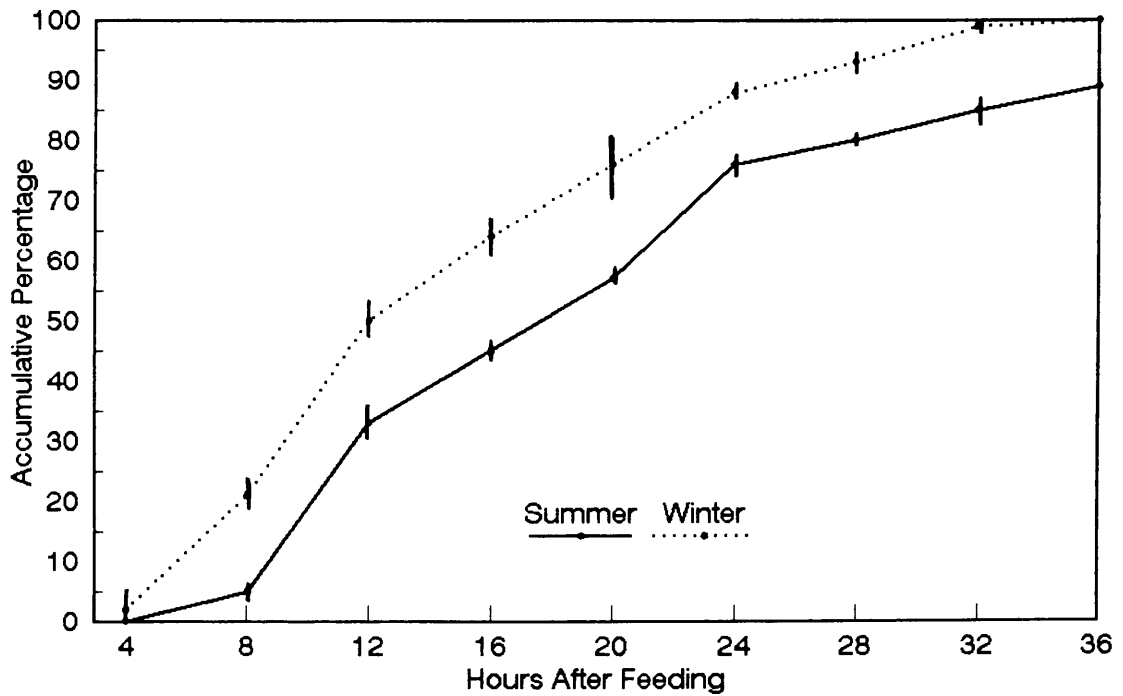
Fig. 18. Mean passage times (h) of digesta marked with plastic
pieces in X. inauris in summer and winter. N=6.

Table 24. The mean hindgut dimensions and maximum gut section volumes of X. inauris. n = 8. Mean ± standard deviation.

GUT SECTION	GUT MASS g	% OF TOTAL MASS	GUT LENGTH mm	GUT VOLUME ml
STOMACH	24,86 ±4,30	27,50	62,38 ±8,00	20,84 ±3,92
SMALL INTESTINE	21,58 ±2,75	23,87	805,00 ±97,8	37,37 ±6,78
CAECUM	29,06 ±3,49	32,15	102,25 ±21,25	18,06 ±1,42
COLON	14,89 ±3,12	16,47	37,88 ±6,78	23,63 ±1,79

The large intestine could be divided into four sections based primarily on external characteristics. The first two sections were found in the caecum. Although the caecum was not significantly (t=1,75; df=14) larger in volume or mass than the stomach, it was the dominant structure of the digestive tract and when weighed, it's mass exceeded that of the stomach (Table 24). When the body cavity was opened by ventral incision the caecal structure filled the posterior half of the cavity and concealed the other organs beneath it. The caecum had a pH of 7,0 ± 0,3, and consisted of two parts, the ampulla ceci into which the ileum enters and from which the proximal colon emerges, and the corpus ceci which terminates in a blind sac, the apex ceci (Fig. 15). The ampulla ceci possesses a single narrow tenia forming two large haustra. The tenia widens in the corpus ceci where two more haustra of more constricted appearance are located.

The other two divisions of the large intestine are in the colon, the two proximal colonic loops (colon majus) being 297,0 ± 3,8 mm in length and the distal colon-rectum (colon minus), measuring 80,0 ± 2,0 mm (Table 24).
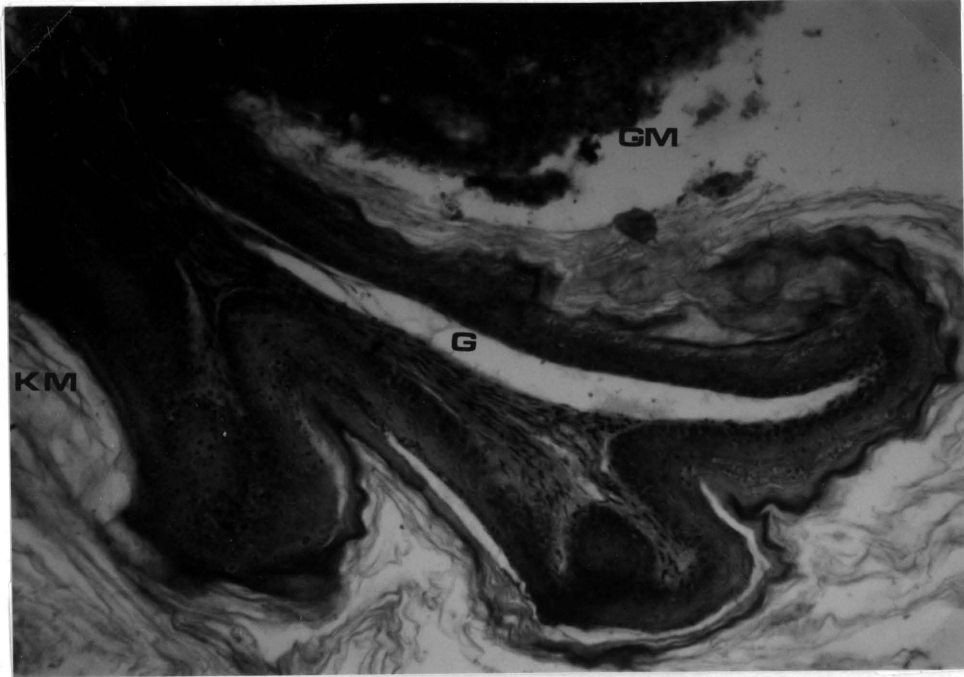
Plate 1. Section of the grenzfalte, showing the demarcation between the keratinized non-glandular corpus and glandular antrum of the stomach of X. inauris. G=grenzfalte; GM=glandular mucosa; KM=keratinized mucosa, 100x.
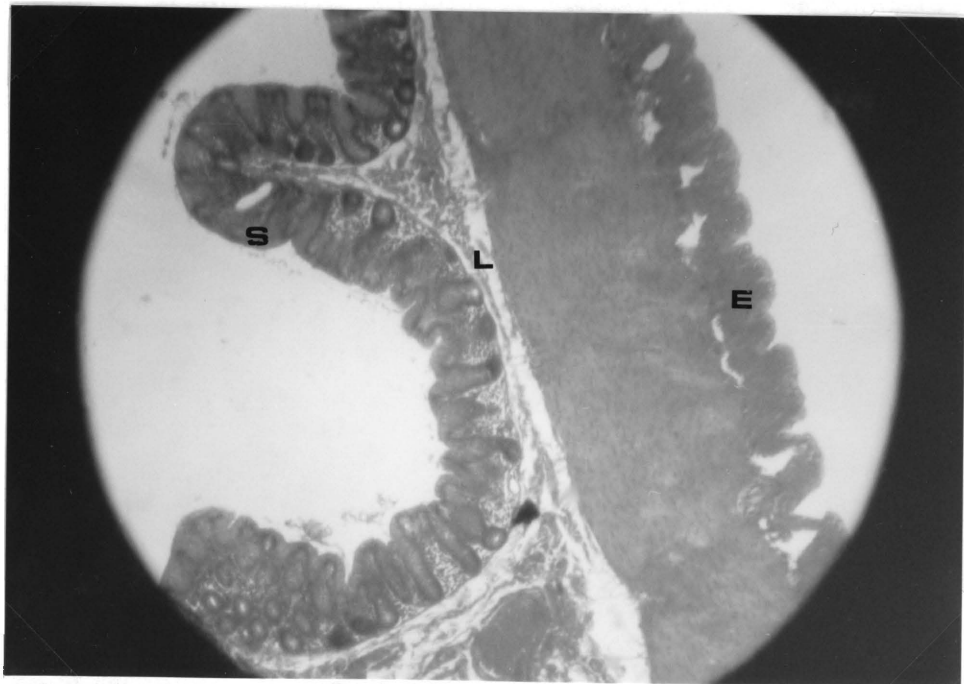
Plate 2. Glands of the folded glandular fundic antrum of the stomach of X. inauris. S= glands; L=lamina propia; E= muscularis externa, mag. 25x.
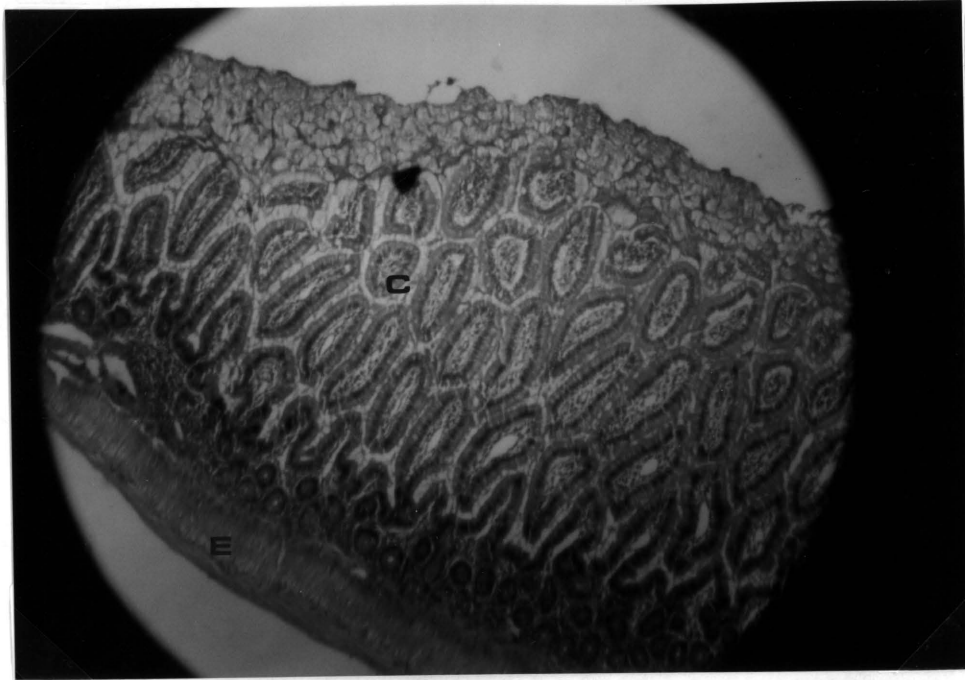
Plate 3. The duodenum (small intestine) region of X. inauris characterised by abundant vilii, supported by a thin muscularis externa, C=crypts; E=muscularis externa, mag. 25x
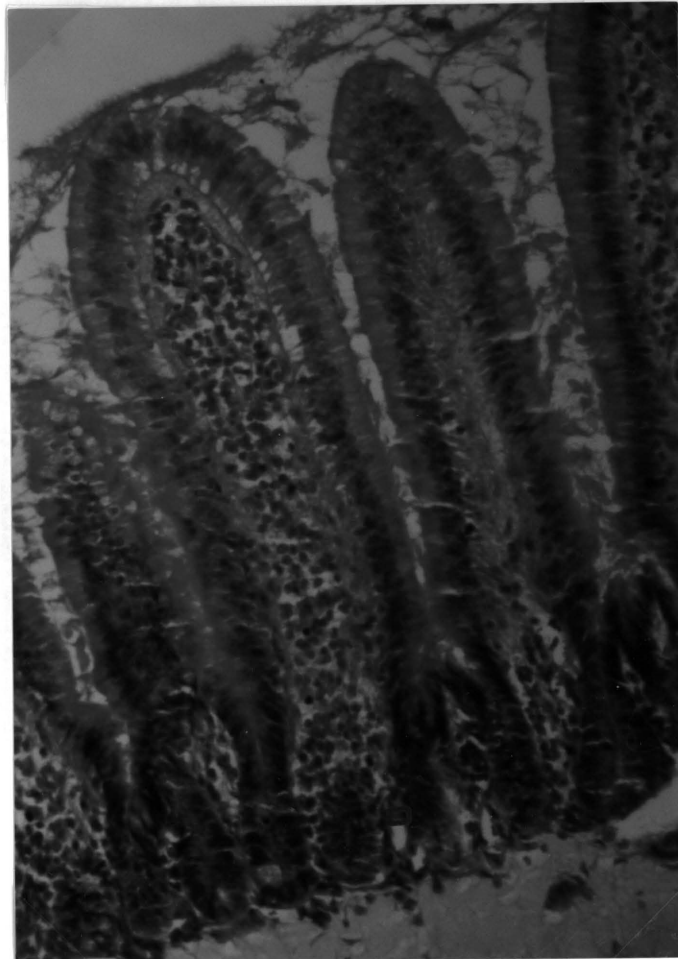
Plate 4. Section of the ileum of X. inauris, showing finger-shaped villi (v), crypsts of Lieberkuhn and goblet cells =O, mag 100x.
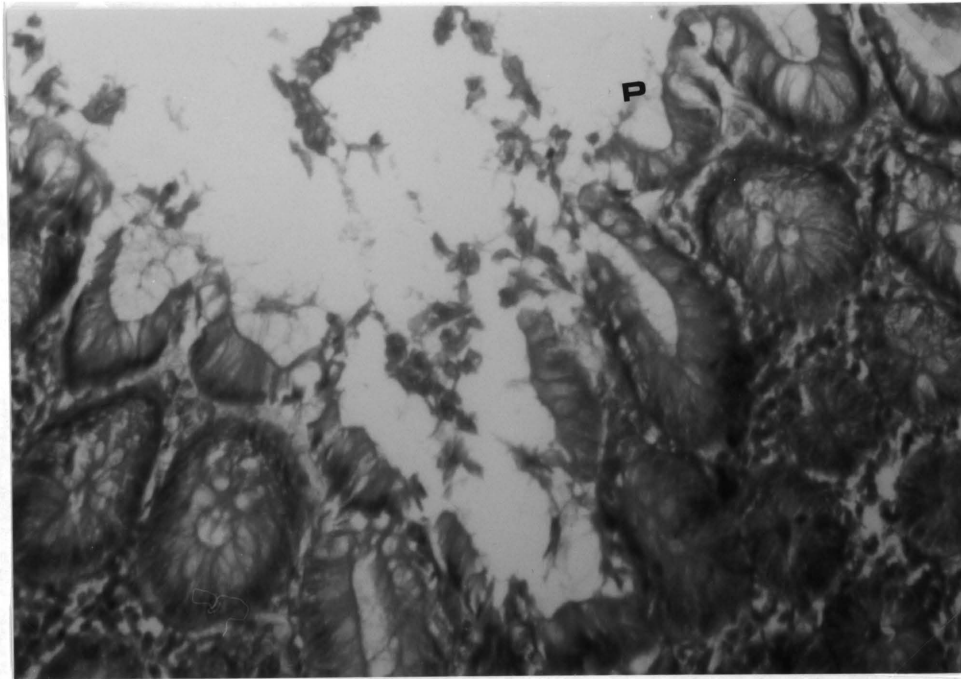
Plate 5. The open crypts of the caecum surface epithelium of X. inauris. open crypts= P, mag 100x.
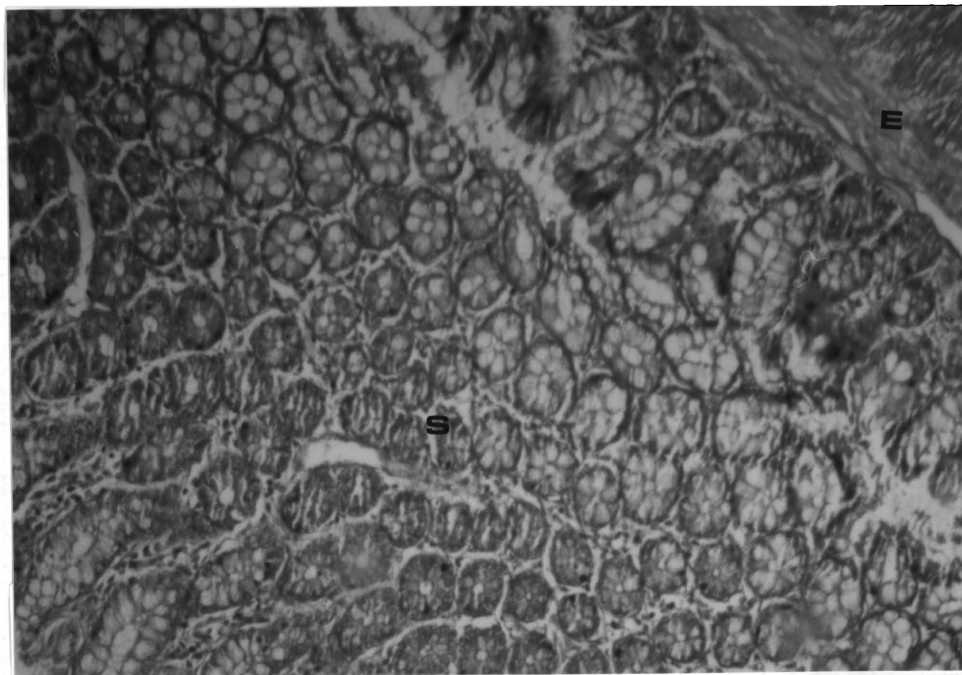
Plate 6. The simple tubular glands (crypts of Lieberkuhn) of the colon of X. inauris, regularly arranged in rows. S=glands; E=muscularis externa, mag. 100x.

Microscopic   morphology

Stomach

With the exception of the epithelium, X. inauris possess a typical mammalian stomach tissue plan (Dearden 1969, Madge 1975). The non-glandular corpus and fornix ventriculi are covered on the lumen side with numerous papillae lined with stratified keratinized epithelium. The Tunica muscularis of the corpus and fornix consists of an inner circular and outer longitudinal muscle layer (Fig. 16). The Grenzfalte separating the glandular and non-glandular regions is keratinized on the corpus side and glandular on the opposite side (antrum) (Plate 1). The corpus (surface area= 1506,8 $\pm$ 102,0 mm^2) is significantly larger than the glandular antrum (surface area= 714,9 $\pm$ 141,0 mm^2) (t = 14.28; df = 10; P < 0,001).

In the glandular antrum, the passage of foodstuffs is delayed and food is subjected to enzymatic and hydrolic action of gastric juice. The antrum is lined by simple columnar mucus-secreting epithelium containing gastric pits which dip down to form glands (Plate 2).

Three distinct gastric regions, the fundic, cardiac and pyloric gland regions can be identified. The Tunica mucosa of the fundus was found to be the thinnest of all the stomach mucosa regions (t= 4,5; df = 11; P= 0,001). Furthermore, the fundus consists of simple and branched tubular glands with mucoid cells on the upper sides of the foveolae. The mucus that is excreted protects the fundic glands from the hydrolic action of the HCl (hydrochloric acid). The chief (zymogenic) cells produce the gastric enzymes and the parietal (oxcyntic) cells at the body of the pits of the glands, elaborate HCl.

The Tunica mucosa of the compound tubular glands of the cardiac region is comprised of simple columnar, mucus-secreting cells, which is similar to the other three proper gastric regions, excluding the fundus area (Fig. 19). The

cardiac Tunica muscularis was 0,691 ± 0,11 mm wide, and intermediate in the range of stomach muscle widths.

The distal pyloric region, consisting of simple, short branched tubular glands, secretes mucus and enzymes. Although not significant (t=1,9; df=11; P= 0,077; t= 1,5; df=11; P=0,089), the Tunica mucosa and muscularis layers of 0,607 ± 0,14 and 0,907 ± 0,18 mm respectively were found to be thicker than the cardiac stomach region (Fig. 19). The pyloric sphincter consists mainly of smooth circular muscle.

Small intestine

An abrupt change in the character of the mucous membrane occurs at the gastro-duodenal junction, where gastric pits are replaced by villi. Proximally the duodenum is thicker (t=2,9; df=11; P=0,001), as large and numerous tongue-shaped villi protrude from the numerously folded plicae. Intestinal crypts are prominent (Plate 3).

The jejenum is similar to the duodenum but villi are thinner, smaller and fewer. Villi in the ileum are finger-shaped and less numerous on fewer plicae. The epithelium consists entirely of goblet cell and other epithelial cells such as Paneth cells. The Tunica mucosa is significantly thicker (F=12,89; df=28; P=0,001) than that found anywhere in the intestines (Fig 20), while the Tunica muscularis is thinner, although not significantly so (t=1,92; df=28; NS) than all the parts measured (Plate 4).

The secretions of many glands are added to the food material in the lumen of the small intestine. These glands are of three types: the intestinal glands, the submucosal glands (Brunner glands) and the glands situated outside the digestive tract (liver and pancreas) but passing their secretions into it's lumen by a duct system (Banks 1986). Intestinal secretions contain bile, enzymes
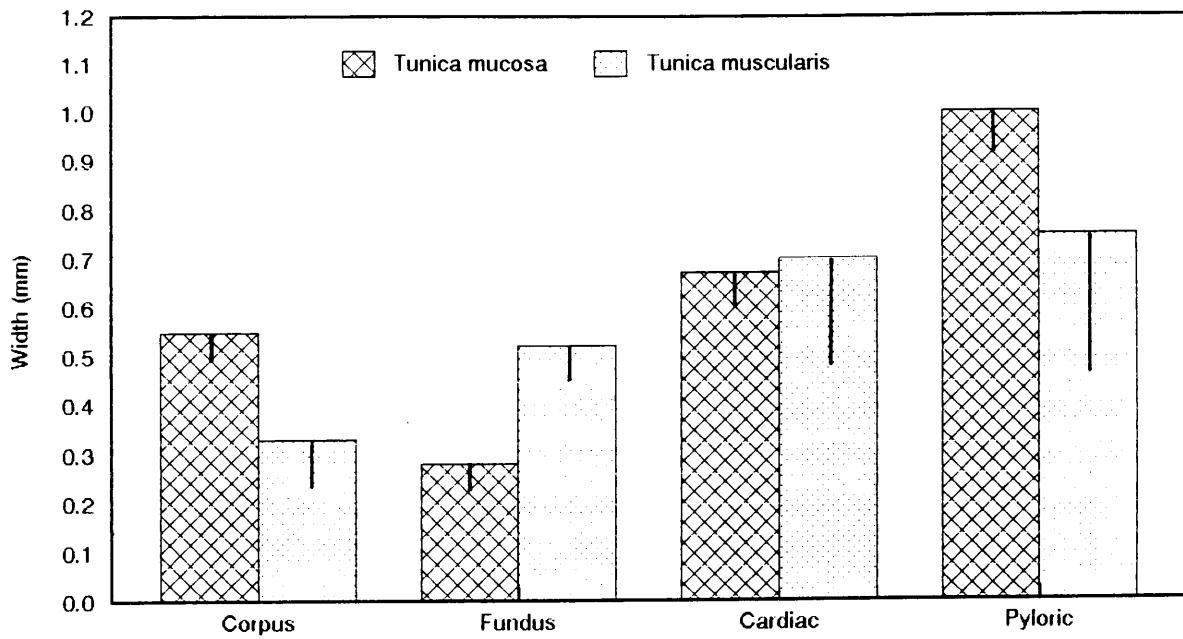
Fig. 19. Thickness (mm) of the Tunica mucosa and Tunica muscularis of the stomach of X. inauris. Bars = SD.
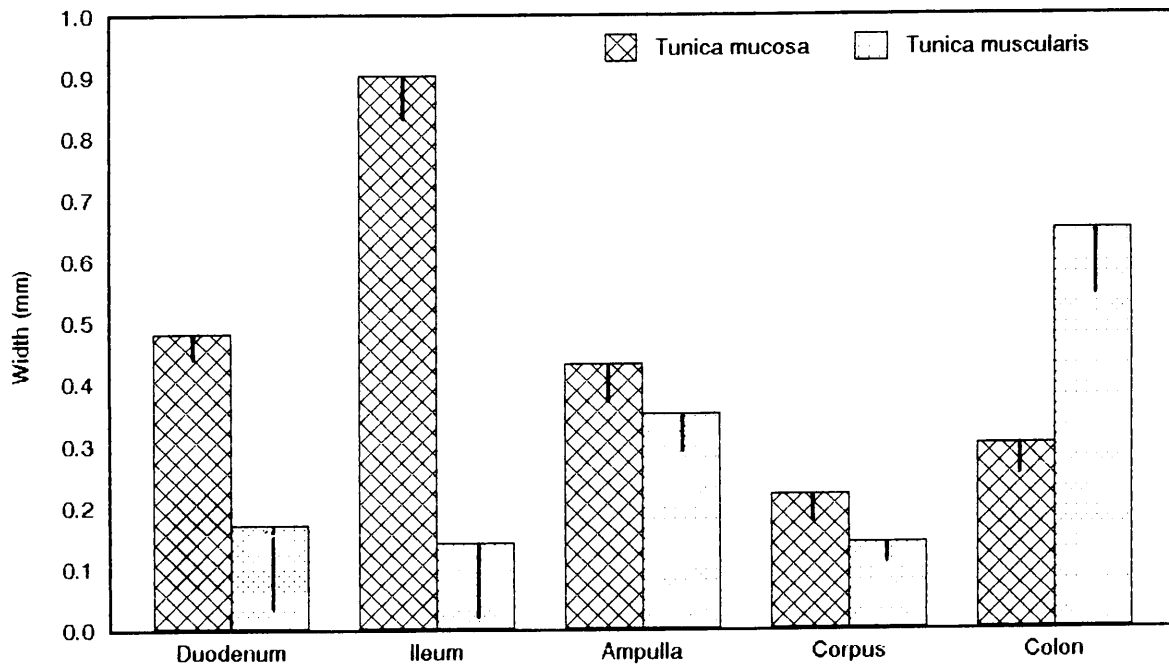
Fig. 20. Thickness (mm) of the Tunica mucosa and Tunica muscularis of the hind gut of X. inauris. Bars = SD.

(lipase, maltase and peptidase) and mucus, which reduces the molecular size of food material. Absorption of amino-acids and lipids takes place via the intestinal epithelium.

Caecum and colon

The ampulla ceci a blind-ending sac, is the thickest portion of the caecum proper, owing to a significantly thicker ($t=2,88$; $df=11$; $P=0,05$) Tunica mucosa and muscularis (Fig 20). Simple, thin tubular and wide-open glands or crypts of Lieberkuhn, are arranged regularly and secrete mucus (Plate 4). The Tunica mucosa and muscularis of the corpus ceci is thinner than that of the ampulla but the Tunica mucosa is morphologically similar to that described for the ampulla. Digesta enter the caecum in a semi-fluid state, and become semi-solid, the consistency of faeces in the colon. Apart from functioning in fluid absorption, protozoa and bacteria are present, promoting fermentation of fibrous digesta. No digestive enzymes are secreted in the large intestinal parts.

The proximal colon Tunica mucosa is thicker than that of the caecum ampulla or corpus (Fig 20). Plate 6 illustrates the wide area of columnar epithelium and goblet cells of the Tunica mucosa, forming some elongated crypts giving the colon an appearance much like the ileum. Towards the rectum the intestinal glands become short and disappear in the anal canal. Absorption of water from the faeces takes place in this region.

Rate of passage

The mean times of occurrence of 10, 80 and 100 % of the plastic markers in the faeces during the winter trial were found to be $5,5 \pm 1,9$; $21,5 \pm 2,1$ and $32,0 \pm 1,0$ h respectively. This was significantly faster ($t=2.9$; $df=14$; $P < 0,05$) than

the summer trial of 9 $\pm$ 2,5; 32,0 $\pm$ 4,0 and 40,0 $\pm$ 5,5 h respectively (Fig 18). A mean retention time of 30,2 h was calculated from the integrated average time between marker ingestion and excretion. The time interval between the first and last appearance of plastic pieces for both winter and summer trials averaged 7,0 $\pm$ 0,5 h and 38,5 $\pm$ 1,5 h respectively.

DISCUSSION

Hypsodontic molars are indicative of herbivory and, as postulated by Vorontsov (1962), such molars facilitate grinding more fibrous foodstuffs. X. inauris has a stout skull with inflated bullae and a single premolar is present in each jaw, followed by three hypsodontic, laminated molars (De Graaff 1981). They are herbivores, making use of the best available foodstuffs and during the cold-dry winter, their diet becomes more fibrous (Chapter 3).

The transit time of food stuffs with low fibre content in porcupines (H. africae-australis) was between 23 and 64 h (Van Jaarsveld 1983), which was comparable to the 30 to 44 h found for X. inauris feeding on a low fibre diet. The faster transit times of food in winter acclimatized squirrels were a result of a higher intake of food during the winter trial due to higher metabolic needs. Rapid food passage depends on the kind of food available together with its digestibility and can have many advantages. The ability to consume, digest and excrete food in a short time would mean that X. inauris would have more energy available for eg. an emergency response. Fast passage rates could be associated with the lack of hoarding behaviour. If the animals had slow passage rates, then a glut of food might enhance tendencies to store it for later consumption (Chapter 4). For X. inauris the cost of activity during winter increased by 32,0 % and this extra energy demand had to be balanced via ingestion of more fibrous foods and roots as well as efficient digestion (Chapter 5). The possibility of a slower passage

rate cannot be excluded, but the potential enlargement of the caecum with its fermentative action on the cellulose is more likely during such times.

The unilocular hemi-glandular stomach of X. inauris, is believed to be a primitive condition from which the more complex bilocular discoglandular form evolved (Carleton 1973). The stomach is cornified with the glandular region divided into three areas. This makes it more complex than it appears when investigated superficially. The papillated cornified areas greatly increase the surface area and are comparable to those found in T. paedulcus, Mystromys albicaudatus (Perrin & Curtis 1980) and C. gambianus (Knight & Knight-Eloff 1987). The incisura angularis was shallow and no sacculation occurred, as in Saccostomus campestris (Perrin & Curtis 1980). However, over two-thirds of the squirrel stomach mucosa was non-glandular. Two opposing theories exist for the function of the non-glandular corpus in myomorph rodents. The corpus may act as a fermenting forestomach (Vorontsov 1962) or function as a storage chamber where initial and prolonged breakdown of carbohydrates by salivary amylase may occur (Carleton 1973). The latter of the two suggestions is probably applicable to X. inauris. Irrespective of the fact that no fermentative bacteria were detected in this area, with our present knowledge, fermentation could not take place at a pH of 4,5. This large stomach could further be important for maintaining a continous flow of digesta down the tract and could effectively reduce the total foraging time. Proteolytic degradation and some carbohydrate digestion probably occur in the glandular stomach as was found for two cricetomyinae species (Perrin & Kokkinn 1986). The stomach contents of X. inauris had a mass of 3,4 % of the body mass, which is lower than the 6,5 % reported by Van Jaarsveld (1983) for the porcupine, but higher than the average of 2 % for Otomys species (Perrin & Curtis 1980).

The small intestine length is similar to that of P. palliatus tongensis (Viljoen 1980) which is an omnivorous tree squirrel, living predominantly on fruit. Herbivory has been linked to longer small intestines (Vorontsov 1962, Schieck & Millar 1985), but a study on rodent digestive tract morphology, established

that very little variation in small intestine length occurred in 19 different species, although 21 % of them were herbivorous and 79 % omnivorous (Perrin & Curtis 1980). Therefore one could argue that, as environmental conditions change, subtle differences should rather be monitored at the microscopic level. Numbers and height of papillae, glandular pits and villi could possibly change in size to enhance or reduce surface areas, thereby influencing digestion and especially absorption of end-products, without necessarily increasing the gut length.

The X. inauris duodenum could be identified by it's abundant leaf-shaped villi. In the ileum and jejenum, histological differences were slight making a clear distinction between these areas impossible, however, the jejenum region has fewer and thinner villi. Considerable digestive activity may occur in the lumen of the intestine, even though no digestive enzymes are secreted by the intestine itself (enzymes that are secreted is known as the succus entericus and originate from the pancreas and liver). Rodent small intestines are all basically the same and conform to the normal mammalian pattern of a short duodenum leading from the pyloric stomach, and the longer jejenum to an ileum.

The caecum of X. inauris is a large fermentative vat, implicating its possible wider nutritional significance. In contrast, S. carolensis, a granivorous squirrel, (570 g) (Schieck & Millar 1985), possesses a smaller caecum but larger colon than X. inauris. S. columbianus, a herbivore, has a large caecum which is comparable to that of Xerus in size. The ampulla ceci with its thick wall appears to act as a sorting chamber for digesta, directing them from the ileum into the corpus ceci or away from the corpus ceci into the proximal colon, as was found for the rabbit (Oryctolagus cuniculus) (Bjornhag 1972) and giant rat C. gambianus (Knight & Knight-Eloff 1987). Wide open crypts in the corpus ceci, similar to those found in other rodents (Snipes 1979, 1981, Knight & Knight-Eloff 1987), enhance absorption, and specifically water absorption as a conservation factor, through enlargement of surface area (Chapter 7). Furthermore, the detection of protozoa in the lumen underlines the

fermentative action on fibrous digesta in this region. Apart from the role of the caecum in furthering digestion and absorption, its structure appeares to be influenced by its phylogenetics, being closely linked to that of other Sciuromorpha (Gorgas 1967).

In general the caecum is known to be flexible and can enlarge macro- and microscopically (Parra 1978). This classical concept and that most herbivores possess a well-developed caecum has been upset by striking exceptions such as the lack of a caecum in the giant panda (Ailuropoda melanoleuca) a carnivore which developed subsequently a herbivorous way of life (Davis 1964). Within the Rodentia several carnivorous species such as Deomys and Hydromys (Behamm 1973) possess caeca. Snipes (1979) concluded that phylogenetic factors also determined the potential development of the caecum, but that it in turn could be affected by factors such as changes in available foodstuffs and dietary habits. Although such changes could not be measured during the present study, it is assumed that this feature could be of great importance in X. inauris when food resources change or diminish in an unpredictable environment.

The colon functions as an area where water and electrolytes are absorbed and is associated with fat deposits. Here the pellets are formed and stored and the abundant mucus-secreting cells lubricate their passage. As in other arid-adapted species (Forman & Phillips 1988) water recovery and conservation by X. inauris during periods of water shortage, could be simulated during some water deprivation experiments (Chapter 7). Faeces of squirrels were reduced in quantity and were drier when animals were water deprived. Although no coprophagy was observed, caecotrophy, i.e. the ingestion of normal faeces and recycling of microbial protein in the foregut of X. inauris could not be excluded. In other rodents this form of ingestion has been observed and was stimulated by season, the type of food eaten and adverse feeding conditions (Cork & Kenagy 1989, Woodall 1989).

Summary

The idea that rodents are fundamentally herbivorous was negated by Landry (1970). He suggested they were omnivorous at first, becoming specialised towards insectivory and herbivory, opposing Vorontsov's (1962) ideas. The evidence of specialization in the gut of X. inauris, although not equivalent for the various parts, could be the result of functional compensation (Vorontsov 1962). The fairly complex stomach may compensate for the less specialized caecum and hindgut. Adapted herbivores do not possess extreme degrees of specialization in all proportions of their digestive systems. Thus it is possible to conclude that the compensated organ might become the compensating one (Perrin & Curtis 1980). If such adapted herbivores are compromised by a sudden change of habitat and climate, they may be able to adapt by transformation of certain parts of their gut. The lack of water, comparable passage rates with other monogastric mammals (Parra 1978, Milton 1981, Van Jaarsveld 1983, Chilcott & Hume 1985) and large fermentative caecum, provides flexibility in utilizing different food types in the event of food depletion or shortages. X. inauris are opportunistic feeders colonizing the semi-arid to arid areas of Africa. They show some specialized adaptations towards herbivory in their stomach and caecum morphology. No major specializations are found in the digestive tract of X. inauris, however the stomach is divided into a storage and acidic unilocular hemi-glandular organ where absorption of soluble sugars can enhance the availability of energy, and the caecum is large, and contains protozoa and bacteria for fermentation of cellulose. During adverse periods of low rainfall when the herbage is dry, fibrous and nutritional levels are depleted, X. inauris could possibly survive on such foods by fermenting them in the large hindgut.

CHAPTER 7

WATER TURNOVER IN FREE-RANGING AND LABORATORY ACCLIMATIZED SQUIRRELS.

INTRODUCTION

Two essential resources required by animals are energy and water. Together they compose the main selection pressures in terrestrial environments (Edney & Nagy 1976). Animals in an arid environment need to minimize their water expenditure. Water is continually lost from the bodies of animals through evaporation, respiration and excretion and this loss needs to be balanced by water intake via oxidation of food, water in the food (eg. succulent plants and insects) and from drinking. Furthermore, the capacity to concentrate urine and minimize urinary and faecal water loss, in conjunction with lowered respiratory water loss contributes to the maintenance of a positive water balance.

Numerous studies (mainly on rodents) have revealed that small mammals, particularly those in arid environments, employ elaborate physiological and behavioural mechanisms to conserve water. Elaboration of these water conserving mechanisms tends to be inversely related to the availability of water. Some studies have included water turnover experiments in the wild, but most have been carried out in the laboratory (eg. McNab & Morrison 1963, Macmillen 1972, Macmillen & Christopher 1976, Zervanos 1977, Grubbs 1980; Withers, Louw & Henschel 1980, Degen 1986, Buffenstein 1985a & b, Buffenstein & Jarvis 1985a).

Rodents, being burrowers, avoid the extremes of desert environments. X. inauris occupy burrows in a variety of habitats ranging from the mesic northeastern Cape to the semi-arid Kalahari desert (De Graaff 1981) (Chapters 1 & 2). Seasonal climatic variations are common and squirrels must contend with hot

mesic summers and considerably colder, very dry winters. To these small herbivorous mammals that are active throughout the year, such contrasting seasons impose numerous demands in terms of energy and water. High summer temperatures may restrict activity and increase water loss through evaporation, while the lower winter temperatures probably increase energy requirements. Water and energy availability, however, would be reduced owing to a decline in food quality and quantity. Apart from being burrowers avoiding the heat and cold, Marsh et al. (1978) found that X. inauris have very efficient kidneys reflected in a high urine:plasma concentrating ratio.

The following two broadly based questions were then asked:
1. Is there a large seasonal variation in water metabolism in free-ranging X. inauris ?
2. To what extent can water deprived captive X. inauris change their water conservation mechanisms ?
To answer these, a study was carried out primarily to measure patterns of tritiated water turnover rates, hematocrit percentages, urine osmolarity and faecal water contents of X. inauris living under natural and laboratory conditions. Winter acclimatized squirrels were used in the laboratory study.

The discovery of tritiated water (HTO) as a useful chemical for measuring total body water (Pace & Rathbun 1945) enabled the study of daily water exchange and overall state of water economy of an animal. Using HTO, one can measure the rate of body water utilization per day, including intake of water and metabolic water. Rates of water influx (WI) and efflux (WE) in free-living animals are determined with ^{3}H labelled water by monitoring the decline in istope activity over time. As the animal loses labelled water by evaporation and excretion, this is replaced by unlabelled water from the food, free water from drinking and oxidation and the specific activity of the isotope is reduced (Grenot & Buscarlet 1988). To apply the isotopic water method several assumptions are made : 1. the experimental subject is in a steady state of body composition, i.e. that total body water (TBW) is constant; 2. isotopic water is

distributed rapidly and uniformly throughout the body; 3. isotopic ^{3} H is lost from the body as water; 4. neither isotopic nor non-labelled water enters the body through the lung or skin surfaces (Holleman, White & Luick 1982).

METHODS AND MATERIALS

The study on free-living squirrels

X. inauris were captured during four different periods between 1987 and 1990 in the dry Nossob riverbed during the hot-wet summer in December 1987; the cold dry winters of July 1988 and August 1989 and the hot, dry summer in January 1990 (Chapter 2). Immediately upon capture each animal was identified by a colour code painted on its flank with mercurochrome and/or gentian violet. Their mass was measured with a Salter balance to the nearest gram and their sex noted. During subsequent recaptures their weights were taken to establish if the animals were maintaining a steady-state, as radical shifts in mass are indicative of a water imbalance (Nagy 1975).

On initial capture each squirrel was injected intraperitoneally with 0,1 ml HTO per 100 gram body weight (1 uCi per ml distilled H_2O activity). After the initial injection 40 min were allowed for the isotope to equilibrate with body fluids before 350 ul of blood from clipped toes were collected into 70 µl heparinized capillary tubes. Validation of this period was done on two adult squirrels, a male and female, before the study commenced and it was found that the CPM counts of HTO stabilized 40 min after initial injection.

Subsequent blood samples collected in the same manner, were taken from these squirrels two, four and six days after injection. Animals were recaptured and always released immediately after weighing and blood sampling. Captivity trauma was reduced to a minimum by darkening the capture cage and animals were released immediately after being weighed and bled.

After centrifuging blood samples for three min, packed cell volumes were measured. The capillary tube was then broken and the clear plasma collected. Plasma was transferred from collection capillary tubes to calibrated micropipettes and an exact volume of plasma (40 μl) was then added into a standard liquid scintillation vial containing 4 ml toluene/butyl PBD/PBDO scintillation cocktail and thoroughly mixed. Counting was done on a Hewlett Packard 1500 scintillation counter.

Standards of tritiated water were added to measured volumes of water in a manner identical to the blood samples and counted. A blood sample was taken from each squirrel before the injection of the isotope, to be counted as background.

To check whether any inspiration of HTO took place between members of squirrel groups, two unlabelled squirrels of every group monitored were also captured at two, four and six day intervals and blood samples taken. These blood samples were also treated as described above. The CPM counts were then compared with initial blood CPM's of labelled squirrels and any differences subtracted from calculations of subsequent CPM's of the specific group.

The initial percent body water contents and water turnover rates were calculated using the linear assumption of water increase or decrease with time as calculated by Nagy & Costa (1980):

$$\underline{\text{ml } H_2O \text{ flux}} = \frac{2000 \ (W_b - W_1) \ \text{In}(H_1 \ W_1 \ / \ H_2 \ W_2)}{(M_1 + M_2) \ \text{In} \ (W_2 \ / \ W_1) \ t}$$

H = counts per minute (CPM) per unit volume of body water, corrected for background CPM; W = is body water volume in milliliters; M = body mass in grams.

Environmental and burrow temperatures were monitored during the four study periods. Rainfall was continually monitored at Nossob camp and at the study

area during the four year study period (Chapter 2; 4). Combined rainfall figures of three, nine and 12 months prior to HTO experiments on free-ranging squirrels were correlated with several parameters such as water flux, hematocrit percentages and TBW.

Faecal water content was determined from faeces of field squirrels excreted during the captured period. Faeces were immediately weighed and oven-dried at 60° C to constant weight. During the study in the wild, several samples of the plant species squirrels were observed to feed on were collected and dried to obtain water content.

During July 1988 eight squirrels were sacrificed to obtain samples. Kidney masses and dimensions (width and length) were taken. Urine samples were also collected from the bladders of these animals to determine osmolarity with a Wescor OM-230 B osmometer (Scientific Associates, Cape Town).

The laboratory study

During January and August 1989, two sets of six acclimatized squirrels were trapped near Nossob camp. During January (hot-wet summer period), animals were taken to the laboratory where they were kept under natural photoperiod at day and night room temperatures of 29° C and 22° C respectively. The experimental group captured during August (cold-dry winter period) was kept at 18° C during the day and 10° C at night. Squirrels were housed individually in stainless steel cages with shredded paper for nesting material and animals were fed a dry rodent ration (Cerebos Food Corp. Ltd., Wadeville) mixed with water so that the mixture contained 81% water by mass during both the January and August experimental periods. These squirrels were fed the diet immediately after capture for 6 days at Nossob camp. The squirrels were then transported to the laboratory where their water turnover was measured over another 6 day period. The rodent ration energetic value was 16,3 kJ/g. A gram of the ration

contained 16 % protein, 54 % carbohydrates, 15 % fibre, 8 % fats and 7 % minerals. No ad lib water was provided.

Squirrels were injected within two days of arrival with HTO and subsequent blood samples were taken three and six days later. These blood samples were centrifuged and plasma analysed for radio-activity as described for the free-ranging study. Simultaneously the digestible energy expenditure, urine excretion and osmolarity were measured for the six day duration of the isotope experiment. Food consumption was determined by initially (first two days before the HTO experiment started) supplying a known quantity of food (always saturated with 81 % water) but in excess of daily requirements. All food quantities given to squirrels in the digestion trials that followed were similar, using this information.

After the six day HTO experiment was completed, a 15 day nutritional trial followed in the laboratory, testing the percentage apparent digestibility, urine excretion volumes and osmolarity of squirrels. These were fed the rodent ration containing five different water percentages ranging from 71,0 % to 45,0 % This ratio of deprivation was chosen to ensure total deprivation of 26% within 7 days. During the first three days of the experiment, the diet was mixed with 71,0 % water, the following three days it was mixed with 66,0 % water, followed by three days containing 63,0 % water, followed by three days of 55,0 % water and finally the last three days the food contained 45,0 % water. Unconsumed food, faeces and urine (covered with liquid paraffin) were collected daily. Each urine sample and its mass and volume were noted. Faecal water content was determined by oven drying at 60° C to constant mass. Before each three-day food change, squirrels were weighed to check for mass changes. Food, faeces and urine samples were converted to energy equivalents using an adiabatic CP 400 Calorimeter (Gallenkamp). Benzoic acid with an energy content of 26, 43 kJ/g was used as a standard. Urine samples were freeze-dried before being pelleted for energy content measurements. The water intake of squirrels could be calculated from the water present in the food eaten. Digestible energy

assimilated as kJ/g/day (DEA) was calculated as (energy content of food x mass of food consumed per day) - (energy content of faeces x mass of faeces produced + energy content of urine x mass of urine produced).

Apparent digestibilities (AD) were calculated as AD = GEI - DEA / GEI (100) (Robbins 1983) (GEI = gross energy intake; DEA = digestible energy assimilation).

All values are presented as means $\pm$ standard deviations (SD), with the number of observations 'n'. Statistical tests were either t-tests, paired t-tests where appropriate or standard linear regressions (SAS 1988). A probability of less than 0,05 was taken as the level of significance. The ANOVA procedure was used to test for significance between sexes, seasons and treatments (SAS 1988).

RESULTS

Climate

Field study

Mean maximum summer temperatures averaged well above the winter mean maximum (t=3,9; df=10; P<0,001) (Chapter 2). Rain never fell preceeding and during the study periods and no free-standing rainwater was available to the ground squirrels. However, during the summer of 1989/1990 the summer rains failed and the veld was exceedingly dry. This had a profound negative influence on the vegetation (Table 25).

The results from free-living squirrels are presented in Table 25. As no significant differences were apparent between water turnover rate and sex of the squirrels, the data on males and females were pooled (F=0,03; df= 21;

P=0,8719). All squirrels tested were adults and changes in body mass were not significant between the different seasonal studies (F=1,9; df=21; P=0,269). The average changes that did occur never exceeded 2,5 %. However, body mass was positively correlated with the flux of water (ml/day) (r=0,37144; P=0,0516).

The highest water flux was recorded in the hot-wet summer of December 1987 (Table 25). The rainfall of three months prior to the HTO experiments correlated positively with the water flux of the seasons as ml/day and when body mass was incorporated as ml/kg/day (r=0,57255; P=0,0015 and r=0,52773; P=0,0039 respectively). Hematocrit and TBW correlated negatively with rainfall measured three months prior to the HTO field experiment (r=-0,47539; P=0,0106 and r=0,395; P=0,0372 respectively). No correlation existed between water flux and rainfall measured nine or 12 months prior to capture.

Lumped seasonal data revealed significantly higher TBW percentages in the hot-wet summer acclimatized than cold-dry winter acclimatized squirrels (t=2,08; df=21; P<0,05). A similar correlation between water flux (ml/day) and season was found (F=5,38; df= 2&21; P=0,0311). Although TBW percentages were significantly higher in the summer squirrels of 1987 than the winter squirrels captured during July of 1988 (t=3,59; df=13; P<0,001), no such significant tendencies were measured for squirrels caught during August 1989 and January 1990 (t=0,51; df=11; P>0,05).

Significant differences between seasons of a particular year were found. Summer squirrel water flux was higher than that of winter squirrels (t=3,59; df=13; P <0,001 and t=-2,38; df=11,00; P<0,05 respectively) for both years. Lean body mass (linked to TBW), was significantly higher in squirrels of the combined summer periods than the winter acclimatized squirrels (t=2,26; df=13; P<0,05 and t=2,34; df=11; P<0,05 respectively).

Table 25. **X. inauris** body water content, water turnover, percentage hematocrit (N=28) related to rainfall measurements during four experimental periods between 1987 and 1990

	Dec 1987	July 1988	August 1989	Jan 1990
No. of animals	9	6	7	6
Body mass (g)	619,6 ± 85,2	595,4 ± 60,5	627,4 ± 52,0	645,0 ± 47,0
[a] Lean body mass (g)	596,9 ± 43,7	505,9 ± 51,0	561,9 ± 31,7	601,4 ± 20,1
Average % mass change	2,3 ± 1,0	2,1 ± 0,8	2,5 ± 0,9	1,3 ± 0,3
Percentage total body water (TBW)	70,3 ± 5,2	62,0 ± 3,9	65,4 ± 5,0	68,1 ± 2,3
Turnover ml/kg/day	55,9 ± 12,0	36,7 ± 11,5	47,8 ± 13,0	39,5 ± 9,4
Turnover ml/day	34,7 ± 6,8	21,8 ± 6,8	29,9 ± 4,2	25,5 ± 2,2
[b] Predicted intake (ml)	68,4	66,0	69,2	70,9
[c] Body water proportion exchanged/day	7,8	5,9	7,3	5,8
[d] Percentage fat	3,7	15,0	10,4	6,8
Percentage hematocrit	45,6 ± 2,3	50,3 ± 1,9	49,2 ± 6,7	53,1 ± 5,5
Previous 3 months rainfall (mm)	63,7	0,0	0,0	2,5
Previous 9 months rainfall (mm)	71,2	304,0	36,5	267,3
Previous 12 months rainfall (mm)	168,5	312,2	294,3	134,8
Average plant water (%)	78,7	39,3	35,2	28,1
Faecal water content (%)	56,2	44,1	45,5	42,0
Average maximum(° C) daily	35,9 ± 3,5	23,6 ± 6,5	27,1 ± 7,8	38,3 ± 3,0

[a] Lean body mass (LBM); (True TBW (g) / 100)/0,73 = LBM (Pace & Rathburn 1945)
[b] Predicted water intake : $WI = 0,21 \ bm^{0,9} \ ml$ (Adolph 1949, Hudson 1962).
[c] water proportion; (flux (ml/day) / TBW)100 = x; (x /body mass) 100
[d] % Fat ; TBW/0.73 = x; 100 - x = fat (Pace & Rathburn 1945)

The water content of plants preferred by squirrels changed during the seasons and was significantly higher during the summer of 1987 than the winter of 1988 ($F=4,46$; $df=1\&34$; $P<0,001$) but the reverse was true for the summer of 1990 and the winter of 1989 ($F=2,08$; $df=1\&22$; $P<0,05$).

During the summer of 1987, faeces from the wild squirrels contained more moisture ($t=6,68$; $df=10$; $P<0,001$) than those of the winter of 1988, while winter faeces of squirrels in 1989 were moister ($t=3,99$; $df=7,0$ $P<0,001$) than the summer faeces of 1990. When the faecal data of the winters and summers were combined, faecal water percentages did not differ between the two winter experimental periods ($t=-1,41$; $df=6$) (Table 26).

Seasonal hematocrit percentages of squirrel blood did not differ significantly ($F=0,13$; $df=1\&2$; $P=0,719$) (Table 25).

Laboratory study

a. Water turnover

Laboratory acclimatized squirrels showed no significant differences in mass between seasons ($t=0,81$; $df=10$; $P<0,05$). The average body mass change during the six day HTO trials when squirrels were fed on food containing 81,0 % water, was 0,5 % and 3,0 % for summer and winter acclimatized squirrels respectively. Lean body mass was 12,1 % and 17,0 % lower than total body mass for summer and winter squirrels respectively and did not differ significantly between the seasons ($t=0,31$; $df=10$; $P=0,015$) (Table 26).

Although the TBW of summer acclimatized squirrels was on average 3,8 % higher than winter acclimatized squirrels, no significant difference was found between them ($t=0,95$; $df=10$; $P=0,05$). The flux of water in winter squirrels was significantly ($t=-2,80$; $df=10$; $P<0,001$) higher than in summer acclimatized

Table 26. Body water content and turnover in summer and winter acclimatized squirrels fed on a diet containing 81 % water. Standard deviations in parentheses.

	SUMMER	WINTER	T-TEST
No. of days	6	6	
No of animals	6	6	
Mean body mass (g)	563,2 (46,6)	551,4 (75,7)	NS
Average body mass change (%)	+ 0,5	+ 3,0	--
[a] Lean body mass (g)	494,7 (40,9)	457,5 (33,4)	NS
[b] Percentage fat	12,0 (7,2)	17,3 (5,0)	NS
[c] WI 0.21 $mb^{0.9}$ ml/day	62,8	61,6	NS
Total body water (TBW) (%)	64,1 (6,2)	60,4 (4,3)	NS
HTO flux (ml/kg/day)	66,5 (5,8)	106,2 (19,2)	-5,23; df= 10; P< 0.001
Flux (ml/day)	37,3 (3,3)	59,5 (16,2)	-2,89; df= 10; P< 0.001
[d] Proportion of body water exchanged as flux	10,3 (0,8)	17,9 (5,8)	-3,75; df= 10; P< 0.001
Percentage hematocrit	42,3 (6,3)	48,7 (5,0)	NS
Water taken in via food (ml)	34,6 (9,3)	47,7 (7,4)	-6,26; df= 10; P< 0.001
Urine excreted (ml)	33,8 (1,6)	46,7 (2,2)	-3,53; df= 10; P< 0.001
Faecal water excreted (ml)	2,5 (0,3)	3,5 (0,4)	NS
Total excreted (ml)	36,3 (1,5)	49,2 (1,5)	-6,70; df= 10; P< 0.001
Urine osmolarity	2000,0(350)	2800,0(200,0)	16,63; df= 10; P< 0.001
Gross energy intake (kJ)	685,00 (38,0)	941,5 (36,0)	-11,85; df= 10; P< 0.001
Faeces excreted (kJ)	69,20 (7,0)	93,0 (7,2)	NS
Urine excreted (kJ)	9,40 (2,1)	10,7 (0,8)	NS
Digestible energy assimilated	606,4 (9,9)	837,8 (10,4)	
[e] WEI (ml H_2O/kJ)	0,061(0,01)	0,064(0,01)	t= -3,91; df=10; P< 0.001
Apparent digestibility (%)	88,5	89,0	--

[a] Lean body mass (LBM) = TBW (g)/100 = x; x/0,73 = LBM (Pace & Rathburn 1945).
[b] % Fat = TBW/0,73 = x; 100-x = fat (Pace and Rathburn 1945)
[c] Water intake = 0,21 bm $^{0.9}$ ml/day (Adolph 1945; Hudson 1972)
[d] Proportion of body water = (flux (ml/day)/ TBW)100 =x; (x/body mass)100
[e] WEI : ml/day/kJ/day

squirrels with 17,9% and 10,3% of total body water being exchanged in the winter and summer respectively. Intake of water was 27,5 % lower in the summer than the winter squirrels and corresponded with food intake. The total water output (faecal and urine combined) was 13 % lower in the winter than the summer squirrels.

Although winter squirrels had on average 13,0 % higher hematocrit percentages than summer squirrels, the difference was not significant ($t = 1,73$; $df = 10$; $P = 0,05$) (Table 26).

The average energy intake per day (kJ) was significantly ($t = -11,85$; $df = 10$; $P < 0,001$) higher for the winter acclimatized squirrels. Faecal and urine energy (kJ) output were not significantly different between seasons but the digestible energy assimilated was significantly higher for the winter than summer acclimatized squirrels ($t = -3,91$; $df = 10$; $P < 0,001$). Apparent digestibilities were similar between seasons and measured 88 % and 89 % for summer and winter respectively.

b. Digestible energy assimilation

During the summer water deprivation experiments, mass of squirrels on a diet with 45 % water content animals declined significantly more than those on a diet containing 71,0 % water ($t = 9,10$; $df = 10$; $P < 0,001$). The mean mass of summer acclimatized squirrels declined by 6,3 % during the 15 day water deprivation experiment, but similar experiments on winter acclimatized squirrels showed a decline of only 2,6 % (Table 27).

Winter acclimatized squirrels ate between 11,8 % and 22,7 % more food than the summer acclimatized squirrels did when subjected to the five different levels of water deprivation ($F = 33,03$; $df = 10$; $P = 0,001$). Apparent digestibility declined by 7,4 % in the summer acclimatized squirrel experiment, but only 4,4 % in the winter experiment.

Water intake declined during the 15 day water deprivation experiment by 53,0 % for summer and 43,0 % for winter respectively. Water intake was significantly higher during the winter than the summer experiment (F=68,15; df=10; P=0,0001).

Total water intake correlated positively with urine output for both summer and winter seasons (r=0,904; P=0,0001 and r=0,763; P=0,0001 respectively). Urine output was not significantly different between seasons (F=0,6; df=10; P=0,443). Urine osmolarity correlated inversely with the experimental food water content (r=-0,6113; P=0,0001). Winter acclimatized animals were found to have significantly more concentrated urine than the summer acclimatized squirrels (F=119,58; P=0,0001) (Table 26).

Faecal water content correlated with the experimental food water contents (r=0,396; P=0,0017). Faecal water content was significantly higher for the winter experiment than the summer experiment (F=26,7; P=0,001). During the summer water deprivation experiment, faecal water loss accounted for between 13,8 and 6,3 % of the total excretory water output, while winter acclimatized squirrels had an output of faecal water of between 35,7 and 20,8 % of the total water output. The combined faecal and urine water output were not significantly different between seasonally acclimatized squirrels (F= 0,85; P=0,3634).

Winter acclimatized captive squirrels showed unexpectedly higher water fluxes of 59,5 ml/day compared to winter field squirrels with 25,4 ml/day.
This was because the laboratory squirrels were fed a hydrated diet which did not imitate field conditions. During winter, squirrels were faced with very much lower water percentages in the vegetation and therefore water turnover results from captive squirrels must be interpreted cautiously.

Table 27. The influence of food water content on body mass, food intake, water output and urine osmolarity in summer and winter acclimatized captive X. inauris.

	71	66	63	55	45
Percentage water in the food	71	66	63	55	45
No. of days	3	3	3	3	3

SUMMER ACCLIMATIZED SQUIRRELS

Mean mass (g)	572,0 (9,0)	568,0 (2,7)	560,0 (2,5)	556,0 (7,2)	536,2 (3,6)
% Weight loss		-1,7	-1,9	-2,8	-6,3
Food intake (GEI) (kJ)	568,0(38,0)	550,2(43,0)	510,0 (3,4)	448,3 (3,3)	428,3 (2,8)
Faeces output (kJ)	42,3 (3,0)	50,0 (6,0)	78,8(12,0)	63,0 (1,2)	60,0 (5,0)
Urine output (kJ)	10,3 (1,0)	10,8 (0,8)	10,5 (0,9)	10,8 (.0,5)	11,2 (0,4)
ᵃ DEA (kJ)	516,0 (30,0)	477,0(30,0)	422,5(25,0)	386,9(26,0)	357,3(10,0)
% Apparent digestibility	90,8	86,7	83,4	86,3	83,4
Total water intake (ml)	24,0(10,0)	21,3 (5,0)	20,7 (8,0)	15,1 (4,0)	11,8 (4,5)
Urine output (ml)	16,0 (0,5)	14,3 (3,0)	13,0 (0,1)	12,5 (0,5)	6,0 (1,0)
Faecal water output(ml)	2,4 (0,1)	1,4 (0,2)	1,4 (0,3)	0,9 (0,1)	0,4 (0,2)
Urine osmolarity (mOsm/l)	2870,0 (9,0)	2920,0(90,0)	3005,0(10,0)	3080,0(40,0)	3350,0(95,0)

WINTER ACCLIMATIZED SQUIRRELS

Mean mass (g)	551,5(14,3)	563,5 (7,4)	552,0 (7,8)	538,0 (9,7)	537,0 (8,0)
% Weight loss		--	--	-2,5	-2,6
Food intake (GEI) (kJ)	29,7(46,0)	616,3(53,0)	613,6(53,0)	597,3(15,0)	565,1(12,0)
Faeces output (kJ)	56,8 (1,5)	56,2 (4,5)	61,7 (2,7)	67,9 (4,1)	72,1 (2,7)
Urine output (kJ)	10,4 (1,0)	11,2 (1,4)	10,3 (1,4)	12,2 (1,0)	13,2 (0,9)
DEA (kJ)	562,0(30,0)	548,9(40,0)	541,0 (19,0)	517,2(10,0)	579,2(11,0)
% Apparent digestibility	89,3	89,0	88,2	86,6	84,9
Total water intake (ml)	27,5 (3,0)	25,0 (4,0)	23,5 (3,0)	20,5 (2,5)	15,5 (3,5)
Urine output (ml)	16,0 (1,5)	14,0 (1,5)	12,5 (0,5)	9,5 (0,5)	4,5 (0,5)
Faecal water output(ml)	4,2 (0,1)	3,0 (0,2)	3,5 (0,1)	2,8 (0,1)	2,5 (0,1)
Urine osmolarity (mOsm/l)	3080,0(50,0)	3260,0(60,0)	3580,0(95,0)	3750,0(60,0)	4290,0(95,0)

ᵃ DEA = digestible energy assimilation (kJ); GEI-FEO-UEO = DEA

Free-living summer acclimatized squirrels exhibited water turnover rates similar to the summer acclimatized captive group. Field water flux measured 34,7 ml/day/squirrel during the summer of 87/88 and 37,3 ml/day/squirrel in the laboratory summer acclimatized squirrels.

Comparing the field water turnover results with the laboratory experiments on animals fed on the excess moisture diet of 81,0 % water, there were no significant differences between the TBW percentage of summer acclimatized or winter acclimatized squirrels. Although the turnover data of the summer squirrels corresponded well with the water turnovers of the December 1987 free-ranging squirrels, mass specific influxes (ml/kg/day) were higher for the winter laboratory squirrels than the winter field squirrels (Tables 25 and 26).

DISCUSSION

Field study

Various physiological (reduced metabolism; concentrated urine) and behavioural (avoidance of extremes; food selection) adaptations make rodents very successful inhabitants of deserts. Tritiated water as a tool for measuring water turnover rates in rodents has proved satisfactory (Edney & Nagy 1976, Nagy & Costa 1980, Grenot & Buscarlet 1988). Some understanding of patterns of water use by free-living animals can be achieved by comparing the magnitude of seasonal variations in water turnover with their minimal requirements in the laboratory. The general water flux in X. inauris conformed to turnovers in other rodent species and, as expected, related positively to mass (Table 28).

Gettinger (1984) discussed water metabolism of species of rodents in the light of water independence and water dependence. This is confusing, as all mammals are water dependent, but some more so than others. A better way of expressing

Table 28. Body water content and turnover in 10 species of rodents. Data for each species represents an average for the number of animals indicated (N).

SPECIES	N	Mass	% TBW*	Flux (ml/day)	Author
Peromyscus merriami	7	18,5	61,5	3,7	Holleman et al. 1973
Petromyscus collinus	4	19,0	63,1	0,8	Withers et al. 1980
Dipodomys merriami	13	34,0	70,1	1,2	Yousef et al. 1974
Acomys cahirinus	5	38,3	65,8	5,1	Holleman et al. 1973
Oryzomys palustric	6	75,5	72,7	16,9	Stalling & Haines 1982
Thomomys bottae					
summer	7	99,4	72,4	25,0	Gettinger 1984
winter	9	108,0	68,0	24,0	Gettinger 1984
Dipodomys deserti	9	101,1	70,9	3,2	Yousef et al. 1974
Petromus typicus	3	130,0	70,0	4,4	Withers et al. 1980
Chinchilla laniger	7	412,0	61,0	26,7	Holleman et al. 1973
Xerus inauris					Present study
summer	6	632,3	68,7	30,1	
winter	6	611,4	63,7	25,5	

this phenomenon would be by categorising the tolerance of dehydration in rodents via a threshold of water dependence : called negative storage (Nagy 1987).

X. inauris were often weighed in the field and no significant differences between body mass per season were detected (Chapter 5). X. inauris therefore seem to have no significant annual or seasonal body mass changes, an important phenomenon when testing water flux. Activity time also reflected no seasonal differences and appears to result from a balance between energetic needs, thermal environment and behavioural thermoregulatory abilities (Fig. 5).

Inasmuch as food is the source of water as well as energy, X. inauris appear to remain herbivorous throughout the year. They showed seasonal changes in the degree of vegetation use of varying magnitudes between the different years, which were indirectly related to rainfall (Chapter 3).

X. inauris are adapted to seasonal changes in water availabilty. During winter (cold-dry), when water availability declined, water requirements were lowest, no reproduction occurred and squirrels also showed the lowest water fluxes at a minimum of only $\pm$ 5,9 % of body water being exchanged per day. The fractional moisture content of the vegetation during the summer studies were expected to be higher, but the last summer (1989/1990) proved to be a very dry period, as no rain fell until February 1990 (Chapter 2). This effect plus very high ambient daily temperatures enhanced the dessication of food and subsequently the squirrels caught during this period had lower water fluxes than during any of the other trial periods. The correlation between body water turnover and water availability in the squirrels' natural habitat and subsequent food sources was positive. Consequently, increased water flux could be related to improved rainfall. This has also been found for guinea pigs, gerbils and marsupials (Kennedy & MacFarlane 1971, Holleman & Dieterich 1973). It followed that the ratio of high-to-low moisture content food sources were directly influenced by the availibity of green vegetation. X. inauris primarily

selected vegetation with high water contents. They were noted to pick the softest parts of grass stems or leaves and flowers, fruits and roots of many annuals. Feeding on green vegetation with a high water content can therefore account for high water fluxes (Chapter 3).

X. inauris appear to have an annual cycle of water flux, which is seasonally influenced. During dry years the flux was lower than during wet years. This was also found to occur in American ground squirrels and chipmunks (Blake 1971, Karasov 1983b). Seasonal changes in water flux of free-living X. inauris suggested that the usage of water was not a passive phenomenon. Whilst the cold-dry winter season induces the physiological response from squirrels to conserve water and a subsequent decline of water flux (±25,9 ml/day), the summer flux (±30,1 ml/day) increased. These findings agree with the changes observed in Isoodon macrourus (Hulbert & Gordon 1972) and collared peccaries Dicotyles tajacu (Zervanus & Day 1977) but are contrary to those for D. merriami and Perognathus fallax (MacMillen & Christopher 1975). The unavailability of succulent vegetation all year round probably resulted in the decline in water turnover during winter.

Reid (1967) found that the water content of fat-free tissues is essentially constant and adipose tissues normally contain minimal quantities of water. In the present study, mass including the fat proportion did not differ significantly between seasons, although lean body mass (LBM) was found to differ between seasons. Therefore, to evaluate water turnover correctly, it is probably more valid to use the LBM of animals. The significantly higher summer TBW percentages for squirrels were consistent with an inverse relationship between fractional body water and fat content in animals (Pace & Rathbun 1945, Hulbert & Grant 1983). The TBW percentage of between 70,0 and 62,0 % was comparable to that found for other rodents (Holleman & Dieterich 1973, Alkon et al. 1986). Some fat percentages were higher for both winter periods and a possible build-up of fat in squirrels could not be excluded. S. saturus and Spermophilus lateralis attained a prehibernating fat content as great as 31,0 %

and 18,0 % respectively, the latter being comparable with X. inauris winter fat reserves, but much higher than the 8,0 % recorded for E. amoenus, which accumulates extensive food caches and consequently has no need for such fat reserves (Kenagy & Barnes 1988). Schmidt-Nielsen (1990) gives the energy content of fat to be 39,3 kJ/g^{-1}. If fat energy content was calculated for field squirrels, the animals caught during summer had enough reserves to sustain their DEA in the absence of food for one to two days, while in the winter estimated fat reserves would be sufficient for five to six days. When very cold and cloudy days prevail during winter and X. inauris does not forage, this 'fat reserve' could be an adaptation to meet the physiological demand for energy at this time (Table 30).

Comparing water turnover in X. inauris with the predicted Nagy & Peterson (1988) allometric equation for free-living desert eutherians

$y = 0,145$ body mass ^{0,954}, turnover was only 38,6 and 44,2 % of that predicted for winter and summer respectively. Although these values were lower than the standard water turnover rate for animals of the same size, they were comparable to other desert species such as A. namaquensis and P. collinus (Withers et al. 1980).

Mean hematocrits for 12 species of rodents ranged from 44,2 - 51,0 % (Holleman & Dieterich 1973, Stalling & Haines 1982). Dehydrated Notomys alexis had a 54,2 ± 0,3 % hematocrit (Hewitt et al. 1981). The percentage hematocrit in the summer squirrels of 1990 averaged 53,1 %, possibly as a result of the extreme dry and hot summer and a subsequent decrease in plasma volume.

Faecal water content of desert rodents averaged 50,0 % when deprived of water and resulted from hindgut water reabsorption (MacMillen 1972). X. inauris measured, on average, 44,1 % faecal water content during July 1988, and even drier faeces containing 42,0 % water during the very dry summer conditions of 1989/1990. In contrast, Schmidt-Nielsen (1964) reported non-desert white rats

deprived of water having faeces containing 68,5 % water. However, Buffenstein (1985a) like MacMillen (1972) reported that arid-adapted species such as A. namaquensis and Gerbillurus paeba have faecal water percentages under water deprived conditions of 45,7 % and 46,5 % respectively. Another water deprived rodent, D. merriami, produced faeces containing 45,0 % water (Shkolnik & Borut 1969). Hindgut water absorption takes place between the small intestine and anus and in squirrels this region includes the large caecum, which is followed by the colon. It is suggested that the hindgut of X. inauris is adaptable to food and water regime changes and absorption of water is enhanced by enlarged open crypts (Chapter 6).

The water economy index (WEI) expresses the amount of water (ml) passed per kilojoule of energy metabolized (Nagy & Peterson 1988). This index is similar to the evaluation of water metabolism suggested by numerous authors working on captive animals (MacFarlane & Howard 1972, Yousef et al. 1974, Withers et al. 1980, Nagy 1987, Hinds & MacMillen 1985). The WEI for ground squirrels fed the moist (81,0% water content) rodent diet was calculated. For summer acclimatized squirrels 0,061 ml/kJ metabolized was expended while winter acclimatized squirrels spent 0,064 ml/kJ. These values were comparable to other arid-adapted rodent species such as D. merriami which used 0,068 to 0,183 ml/kJ in the field (Mullen 1971) and was higher than P. collinus (Withers et al. 1980) which resulted in the loss of 0,041 ml/kJ in the laboratory under water deprived conditions. A. namaquensis used 0,098 ml/kJ, which was 36 % more water per kJ than in the ground squirrels (Withers et al 1980). WEI values of desert dwelling species tend to be lower than non-desert species indicating mechanisms for water conservation (Louw & Seely 1982, Nagy & Peterson 1988).

Laboratory study

Although water turnover in the laboratory was consistently higher than in the field, acclimatized summer and winter X. inauris fed on an excess moist rodent

diet showed water turnovers and urine osmolarity which were related to the season of acclimatization. However, the proportion of body water exchanged was 6,0 % lower for summer than winter acclimatized squirrels. Why didn't these results support the field work? The physiological responses with regard to water regulatory efficiency depends on food and thermal constraints. The food was regulated as a balanced diet and the squirrels came from their natural thermal environment, from a cold dry winter period or a hot wet summer period. These physiological controls were tested over a very short period of time and rapid adjustments were shown to relieve water stress. The animals must be capable of detecting internal differences in water balance. However, although we expected winter squirrels to have lower water turnovers than summer squirrels, a paradox occurred. Winter animals ate far more than summer animals, possibly as a consequence of higher energy demands to counteract the cold and being provided with a high energy diet which they did not have to work for. Fat reserves of 17,3 % in winter acclimatized squirrels were 5,3 % higher than those of summer acclimatized squirrels. Surprisingly the general proportions of water being exchanged were low, between 10,0 to 16,0 % of bodymass despite the 81,0 % water content of the diet. The mesic adapted _Microtus_ sp. exchanged up to 60,0 % of its body water daily (Holleman & Dieterich 1973). Low water turnovers can be explained in part by the unusual capabilities of _X. inauris_ to conserve water, specifically renal water. This tendency to continue the conservation of water in the laboratory was also found for _S. tereticaudus_ (Yousef _et al._ 1974).

Using mass related daily water consumption as described by Adolph (1949) and modified by Hudson (1962), an average predicted intake for summer squirrels would be 63,19 ml/day and for winter acclimatized squirrels 62,04 ml/day. Examining these predictions for the DEA experiments on declining water intake (Table 25), a low water intake of 59,0 % lower than predicted, that prevailed in the summer experiment, could be the result of water conservation that still prevails in the summer acclimatized squirrels. The winter squirrels did have

similar to predicted water turnovers, as a result of higher food intakes. The higher intake was a consequence of the cold.

The respective differences of water flux (ml/day) and intake via the food (ml/day) of 2,7 ml and 11,8 ml for summer and winter acclimatized squirrels respectively, makes HTO turnovers useful as an index but not as a measure of water turnover per se. In the latter instance squirrels had a nett intake of 20,0 % water. The magnitude of this possible error is difficult to explain and could be due to several factors. Doubling water turnover nearly halved the error of the rate of exchange (Green & Dunsmore 1978). The six day trial might have been too short a period. The effect of seasons on the physiology of the squirrels certainly affected the laboratory assumptions and therefore makes water turnover experimentation essential in the field.

Osmolarities of 2000 mOsm/l found for X. inauris urine, given the diet containing 81,0 % water, resembles mesic rodent osmolarities. Annual cycling of urine concentration was found for several nocturnal rodents such as D. Merriami, P. longimembris and P. fallax (MacMillen 1972) and seems to be similar for X. inauris. Winter acclimatized squirrels had higher osmolarities (up to 4300 mOsm/l) during the water declining experiment than did the summer squirrels. This phenomenon could arise from preadapted physiological measures as a result of cold, very dry conditions. The food available is low in protein and water and the kidneys therefore are probably concentrating urine, which may have been continued in the laboratory. Most desert rodents have efficient kidneys which enable them to excrete urine of concentrations of up to 3000 mOsm/l (Grubbs 1980, Hewitt et al. 1981, Withers 1982, Goyal 1988) (Table 28). Marsh et al. 1978 reported that due to the exceptional relative medullary thickness of X. inauris kidneys, these squirrels should be able to concentrate their urine up to 6890 mOsm/l. The average water losses per body mass of 0,06 ml/g/day and 0,08 ml/g/day for summer and winter acclimatized squirrels respectively were similar to values for other desert rodents under laboratory conditions (Deavers & Hudson 1978, Withers 1982). The higher

urinary loss in the winter experiments is due to higher food intakes and possibly low evaporative water loss. In summer more water is probably lost in the form of EWL. Because of their relatively 'normal' metabolic rates (Chapter 5), X. inauris might be forced to conserve water by reducing urine volume and increased concentrating abilities for efficient water management.

Seasonality should determine (cool-dry winters; hot-wet summers), the water intake in summer than winter, but that energy requirements would be greater in winter. When squirrels were water deprived, GEI for both summer and winter acclimatized animals declined markedly. Water and kJ intake were higher for winter squirrels than summer squirrels. Summer squirrels under laboratory conditions were probably under greater 'stress' than winter squirrels as indicated by weight loss. Water independance in X. inauris was apparent when food water content was lowered and no other free water was provided. Animals were able to stay in balance, losing little or no weight (2,6 %) during the winter experimental period. However during the summer experimental period, squirrels ate less and as a result this, probably combined with other factors such as reproductive energy demands resulted in a mass loss of up to 4,0 % greater in summer. Similarly, food intake and DEA declined concomitantly with deprivation water in laboratory experiments on P. typicus, A. namaquensis and P. collinus (Withers et al. 1980), G. paeba (Buffenstein 1985b), and rice rats Oryzomys palustris (Stalling & Haines 1982)

Some physiological effort was made to conserve water even though more water was imbibed, since urine volume decreased and osmolarity increased. This suggested that these squirrels must have had high non-renal water losses such as through the faeces. Higher faecal water percentages were measured but not sufficient to account for the low renal losses. Similar results were obtained in Peromyscus (Grubbs 1980). The potential importance of faecal water contents in rodents being a significant fraction of water loss have been overlooked.

Table 29. Body mass(g), percentage fat, fat energy (kJ) and daily kJ intake of
X. inauris fed a rodent ration containing 81 % water.
Standard deviation in parentheses.

Variable	Dec 1989		July 1988		Aug 1989		Jan 1990	
Body mass	619,6	(85,2)	595,4	(60,4)	627,4	(52,0)	64,5	(47,0)
% Fat	3,7	(3,2)	15,0	(6,4)	10,4	(4,1)	6,8	(3,0)
KJ fat energy	900	(180)	3510	(200)	2565	(1300)	1724	(260)
kJ daily intake*	805,5	(180)	774,0	(78)	815,6	(200)	838,5	(260)
Days of survival without any intake	1,1		4,5		3,1		2,1	

* Average daily intake under resting circumstances = 1,3 (0,3) kJ/g body mass

Table 30. Average daily energy assimilation (DEA), resting metabolic rate (RMR), and
activity time above ground of free-living X. inauris during
the two seasons of the year.

Variable	Winter	Summer
DEA kJ/g/day	1,1000	1,5200
RMR kJ/g/day	0,3002	0,3381
Cost while active kJ/g/day	0,7998	1,1819
activity time (h)	6 h 18 min	6 h 40 min
DEA/RMR	3,6640	4,4960
Cost while active/RMR	2,6600	3,4960

Withers (1982) emphasised that the quality of food controls the dietary energy intake and water balance, but also influenced the water lost in the faeces. During the water depriving experiments, faecal water loss for summer acclimatized squirrels declined from 15,0 to 6,3 % of the overall water loss, but the reverse was true for the winter acclimatized squirrels, where an increase of between 20,8 to 35,7 % of faecal water output occurred as water was restricted. The overall water output via the kidneys and faeces did not show significant differences for summer and winter acclimatized squirrels.

As expected, digestibility of food declined between 7,0 and 4,0 % for both sets of acclimatized squirrels when water was restricted. Apparent digestibilities

were generally high for both summer and winter acclimatized squirrels and never declined below 82,0 %. Other workers measured digestibilities of similar magnitude in desert rodents (Buffenstein 1985a, Hulbert & MacMillen 1988). Restriction of water given to H. indica (Alkon et al. 1986) gave varied digestibility results of between 80,0 and 74,0 % How do squirrels cope with the higher cost of activity during winter, considering the cold and poor quality vegetation. First, they make use of behavioural thermoregulatory means of accumulating heat i.e. basking, piloerection, (huddling at night) (Chapters 4 & 5). Secondly, although they depend heavily on preformed water in the food and metabolic water, feeding on low-water containing fibrous grass leaves and stems at this time, they probably supplement their water needs by resorting to roots (Chapter 3 & 4). Thirdly, they concentrate their urine and therefore lower the flux of water (Marsh et al. 1978). Fourthly, the acidic stomach can expand and bulky fibrous foods are stored before breakdown; immediate energy from soluble sugars is therefore available while the low quality food slows down food passage; the large caecum acts as fermentative vat and can store and enhance the breakdown of cellulose (Chapter 6).

Field values of urine concentration and faecal water content were of the same magnitude as laboratory values but, because of the difference in degree of water stress, those of the field squirrels being unknown, these results are probably not comparable.

Water conservation in rodents can be independent of exogenous water sources as long as sufficient food resources can be obtained to meet energy demands. High metabolic water production coupled with efficient water recovery in nasal pasages at lower ambient temperatures, reducing body temperatures during winter and practising hyperthermia during summer, as well as urine concentration, promotes the economic use of water. In addition adaptive behaviours such as basking and huddling in winter and sandbathing in summer, further enhance water conservation.

Table 31. Urine concentrations (mOsm/l) of desert rodents in the field and laboratory.

Species	Mass (g)	FIELD Summer	Winter	Author
Dipodomys merriami	37	3969	1065	MacMillen & Grubbs 1976
Perognathus fallax	21	3797	1300	MacMillen & Grubbs 1976
Meriones hurrianae	70,0	3184	3453	Goyal 1988
Tatera indica	120,0	5128	3700	Goyal 1988
Xerus inauris	560,0	----	3700	Present study
	Mass(g)	LABORATORY Water available	Water deprived	
Dipodomys merriami	33,9	----	3165	MacMillen & Christopher 1975
Aethomys namaquensis	51,8	3490	4835	Buffenstein & Jarvis 1985a
Gerbillerus paeba	juveniles	----	4837	Buffenstein et al. 1985
Tatera leucogaster	----	4753	7767	Buffenstein & Jarvis 1985a
Xerus inauris		81 % water intake	45 % water intake	
summer	563,0	2000	3350	Present study
winter	551,0	2800	4290	

Summary

It could be established that a seasonal variation in water metabolism in X. inauris exists, with the cold-dry winter period being the most demanding. Furthermore, water deprived squirrels changed their metabolism by eating less, concentrating urine, - thereby diminishing urine output, - and having drier faeces. Although winter acclimatized squirrels had a greater food and water intake, the general output of water was very similar between seasons and declined when water was deprived.

Estimated minimum energy requirements could be deducted from the laboratory feeding experiments. When an animals' weight is constant it is in a steady state (Nagy 1975). Likewise, when water loss reaches a minimum in animals in a steady-state, the rate of water flux can be considered the minimal requirement. If we assume that squirrels lost the least water during the cold-dry winter, and that the water flux would be closely correlated with rainfall, both the winter studies gave positive results, making the hypothesis valid. Squirrels only changed 2,0 to 2,5 % of their body mass during the study periods. During both study periods no rain fell the previous three months and squirrel water fluxes were very low, 21,8 ml/day (July 1988) and 29,9 ml/day (August 1989) respectively. The average water flux of the two winter periods, that is the minimal water necessary to maintain a steady state was 0,037 ml/g body mass.

Seasonal annual patterns of water and energy availability differ from year to year in the Kalahari. X. inauris have no choice but to eat fibrous foods in winter, when food quality and quantity declines, and to resort to underground plant storage organs, and take termites. Groups of X. inauris numbers declined during winter probably as a result of poor food resources (not being hoarders). Moreover, poor nutritional quality of available forage might force X. inauris to move to sites of more plentiful vegetation. For example jackrabbits (Lepus californicus), make use of humanly created 'oases' during summer and autumn,

the months of low-quality vegetation in the Mojave desert (Nagy et al. 1976). Likewise, it has been found that X. inauris concentrate next to road edges, riversides and pans where, due to summer rainwater run-off and accumulation, desert plants are green for much longer into the winter season. When conditions improve during summer after the first rains have fallen, X. inauris resume rapid reproduction, resulting in population recovery, with two litters of up to four young during the season, adults fed on the green annuals and established themselves in the centre of pans and dry riverbeds.

Diet selection and behavioural adaptations can be as effective as physiological adaptations in maintaining an integrated nutrient supply and could be employed simultaneously or alone if necessary. Indeed, these seasonal studies have shown that Kalahari desert X. inauris can maximize their rates of water intake by selecting succulent foods. Consequently, the water-conserving power of a species is inversely related to the availability of water in their natural environment (Grubbs 1980, Karasov 1983a).

CHAPTER 8

CONCLUSIONS

In order to fulfil the philosophical obligations of this thesis, this chapter will be devoted to the implications of the findings of the previous chapters.

Thermoregulation, water conservation and digestion.

Mammals and birds are unique in that they continually maintain the extremely high rates of energy metabolism characteristic of endothermy even while inactive or resting. Under arid and hot conditions one would expect X. inauris to have a high rate of water loss and consequent high intake of food as they have no period of seasonal dormancy. However, in addition to using temporal and spatial heat avoidance behavioural patterns during some parts of the day, X. inauris are large rodents and this in itself could lower the overall thermal burden of the hot summers. Physiological control mechanisms are only brought into play under extreme environmental circumstances. Notwithstanding effective urine concentration and faeces dessication, other solutions i.e. relaxing the limits of homeostasis (Chapell & Bartholomew 1981) and circumvention of the problems by behavioural adjustment, burrowing, sandbathing to offload heat, foraging in the shade, practising siesta-time and making use of a parasol tail also make life easier for X. inauris during the semi-desert summers of the Kalahari. Furthermore, the cold was effectively buffered by huddling underground in nests during the very cold winter nights, thereby saving energy. On the other hand, basking, piloerection of hair when above ground and, only emerging when ambient temperatures rose above 15° C also played an important role in survival, in winter.

Behavioural and physiological adjustments used by X. inauris are intertwined and survival mechanisms are ample. The present study not only tried to define what X. inauris is designed to achieve (survival value) but how it does it (mechanisms) (Krebs & McCleery 1984).

X. inauris is ideally suited for its semi-desert existence having developed effective ways of maintaining water and energy balance. These diurnal, herbivorous rodents have excellent capabilities for practising hyperthermia during summer and after moulting, a short, smooth coat that reflects short-wave radiation (Chapter 5). During winter, pelage growth increases, water flux become lower, urine concentrated and faeces drier than during the summer. Perhaps the most striking attributes however, are the behavioural adaptations of minimizing time spent above ground exposed to heat and cold, huddling together in winter (which reduces energy and water output) and selecting nutritious and succulent dietary items (Chapter 3; 4; 7). The large caecum as a fermentative vat digests cellulose using symbiotic micro-organisms (Chapter 6). They have the usual mammalian metabolic performance, but an unusual renal performance, with extreme urine concentrating capacities (Chapter 7). Their efficient kidneys make them virtually independent of free drinking water, water requirement being met from selective feeding soft stems, leaves and roots, their primary energy source.

Behaviour

Although the evolutionary background of X. inauris is complicated by the presence of another closely-linked species, several other questions of significance can be asked. One question of great importance is why does X. inauris live in groups or coteries?

Group size can vary through time, seasonally and annually. Seasonal variation in rainfall and consequent plant productivity could be correlated with temporal variations in the group sizes of X. inauris. Season alone, however, is not the

only factor influencing group size. Although it is probable that females will remain in association with the same individuals for much of their adult life, group size fluctuates daily or even hourly as a result of male movements and emigrations of the younger members of the group.

Resource quality and its spatial variation interacted to influence group size. X. inauris aggregated at points of resource abundance, especially during times when food quality declines and the only patches of available green food are on the edges of pans, incipient pans and roads. Such squirrel aggregations are seldom permanent, as each group returns to its own central burrow every evening, even if it meant covering distances of up to one kilometer.

The benefit of reduced search time for a patch of good food for X. inauris was evident when females synchronised their foraging from the central burrow. If groups forage, one would expect that the high ranking squirrels would have primary access to food, subordinates would in such circumstances have to make way for the dominants. The costs of subtle competition between group members cannot be dismissed. It could therefore play an important role in the size of the group. During winter, group sizes diminished, possibly because subordinates leave the group owing to foraging pressure (Hamilton 1971, 1975).

The adults would be the first to go into new areas where plenty of green herbage or bulbs were available, thus improving chances of foraging success for the subordinates as well. For X. inauris group foraging did not only mean a greater likelihood of the discovery of succulent annuals or a patch of Dipcadi bulbs, but it also meant a reduction in predation risks (Hamilton 1971).

Although the dilution effect improved an individual's chance of not being preyed upon, vigilance which allowed the early detection of predators by members foraging, also played a role in reducing risks. They attempt to 'tail-mop' ground predators such as snakes away from the central burrow system. This behaviour presumably reduces predation, especially of their offspring.

The benefit of group living for X. inauris therefore lies in a composite of all benefits and costs of two of the main behavioural attributes, feeding and predator avoidance.

Evolution

The earliest fossil records of rodents belonged to the extinct sciuromorph family Paramyidae and remains are dated as far back as the late Paleocene (57 million years ago). During the Eocene (54-38 million years ago) there was a rapid diversification of squirrel-like rodents while during the Miocene (26 million years ago) all seven families recognizable today occurred throughout the world, except in Australia, Greenland and the central Sahara (De Graaff 1981).

The Sciuridae made their appearance as immigrants in Africa in the early Miocene. These initial forms evolved in isolation in sub-Saharan Africa. The known African squirrel fossils are from East Africa and also include Xerus and Paraxerus (Cifelli, Ibui, Jacobs, & Thorington 1986). Xerus fossils were identified by their expanded ischiums, and iliums being relatively long in comparison with skull lengths. The unspecialised jaw muscles as well as the presence of premolars in the lower jaw are indicative of retention of primitive conditions rather than derived characteristics (De Graaff 1981).

The present day family Sciuridae, to which the terrestrial, arboreal and flying squirrels belong, comprises two subfamilies, the Sciurinae and Petauristinae. Squirrels in southern Africa comprise some six species, of which four are small and arboreal and two larger and terrestrial. The two terrestrial species X. inauris and X. princeps, whose taxonomic status has been the subject of uncertainty, have now been finally recognised as two separate species after two studies on chromosomal congruence and thermoregulation respectively, (Robinson et al. 1986, Haim et al. 1987), confirmed subtle differences. The question still remains why X. inauris are not invading the Nambian western

rocky and hilly escarpment, and what prevented gene-flow between these populations?

Although fossil evidence from the genus Xerus suggests that they could run and move fast, climbing was not mentioned. We can only speculate that X. princeps live in rocky areas because they could climb better, or perhaps just gradually or maybe dramatically they became isolated from X. inauris. This division of X. inauris and X. princeps was possibly caused through isolation by a physical barrier such as a large river, high mountain or a vegetation barrier such as the grasslands of the the Miocene era. The latter development, when the wetlands changed gradually to grasslands could have left some Xerus populations isolated in the rocky hills. This could have had an 'island-effect' on the different squirrel groups. X. inauris was perhaps confined when conditions deteriorated during the Miocene, especially on the periphery near the rocky hills, and crossing to the rocks through a very dry area was impossible. Possible behavioural differences as well as feeding habits at that time could also have played a role in separating the species.

Today both species occur sympatrically in semi-arid Namibia where they show no morphological divergence nor any outstanding social or ecological separation. During the past ± 20 million years, evolutionary constraints only separated them in minor ways. When comparing X. inauris to X. rutilus and X. princeps in their usage of terrain, X. inauris is the only squirrel found in open terrain. This preference for open areas could very well have been the answer to the species separation and X. inauris's success. None of the factors investigated this study could account for the continued separation of X. inauris and X. princeps.

The other question that arises is why X. inauris did not colonize the whole of southern Africa? What prevents them from colonizing adjacent less arid areas. Apart from being mentioned in the diaries of early Cape settlers as being seen 150 kilometers from Cape Town, no other reports on their distribution since

1656 could be traced. Perhaps the 'fynbos' foods were not suitable, the natural crown fire-cycle possibly destroyed the continuous supply of herbage and the terrain in the southern Cape is too rocky to allow for adequate extensive burrowing. The mesic areas of Natal, the eastern Cape and Swaziland are also devoid of X. inauris. This could be a result of the physical barrier of the Drakensberg mountain range that imposes very cold temperatures and a hard substrate, which makes burrowing difficult. Competition with other rodents, as species diversity increases concomitantly with the increase of rainfall isohyets, could also have a deterring effect.

Evolution is opportunistic, and representatives of many diverse phylogenetic groups may adapt to any one habitat, while quite closely related animals could be adapted to very different habitats (Edney & Nagy 1976). As a genus, Xerus is morphologically well suited to a semi-desert environment. This can be ascribed to the presence of its bristly fur, claws on fore and hind paws which are adaptations for digging and a subterranean life. The adaptations towards temperature extremes include the conspicuous parasol tail and dark skin. However, one could simultaneously argue that all these adaptations could make them suited for mesic areas as well. However, the preference for open habitats probably deterred these squirrels from colonizing thick vegetation.

X. inauris probably show shrinkage and expansion of their distribution and range in time, depending on whether the peripheral circumstances allow movement to better vegetation patches. If these patches become too arid the squirrels would probably move back to old areas where underground sources such as Dipcadi sp. tubers exists, and it could be that they are 'geophyte limited'.

When change occurs it is probable that X. inauris would respond subject to the original state of the system, but that disruption of any of the life history patterns would have a 'ripple' effect on their existence as a whole. If 'stress', such as drought, excessive cold, population pressure or even the sudden

increase in predator numbers arises, an assumption can be made that animals would first have an 'alarm reaction', followed by a 'coping' reaction (Rapport, Regier & Hutchinson 1985). In the Kalahari Gemsbok National Park stress imposed by the management or tourism is minimal, but sudden environmental stress such as a drought, occurs from time to time. In such an event, X. inauris have shown that they can cope with the situation. In the face of extremely hot weather and very low rainfall, between 1984-1987, X. inauris survived, although their numbers declined drastically, probably as a result of high juvenile mortality and a lower reproductive rate as a direct result of dwindling food resources. A complete 'collapse' (Rapport et al. 1985) resulting in extinction never occurred. The role of rodents, why, where and how they function is usually underestimated in large conservation areas such as the Kalahari, their role as a herbivore in the food-web cannot be ignored and it is time that the herbivorous small mammal impact on the environment is evaluated.

CHAPTER 9

SUMMARY

X. inauris, are large, diurnal, burrowing, herbivorous and colonial rodents. Their distribution in semi-desert areas of unpredictable rainfall poses several questions about their adaptations to survival: how 'stressed' are these squirrels in what we, humans describe as a stressful environment?

Plants such as T. terrestris provided succulent leaves, stems, flowers and roots throughout the year. Such plant material served as a water and protein source for X. inauris.

The central burrow system was used to overnight in by all group members and for siesta rests. All other burrows in the home area were used on an ad hoc basis for refuge from predators and the extreme temperatures in summer. Any environmental temperatures outside the thermal neutral zone of between 29 and 33° C, placed demands on squirrels' metabolism. It therefore would be advantageous to rest in a burrow system within a stable temperature regime while ambient temperatures are fluctuating.

Minimal resting maintenance for X. inauris was 0,84 kJ/g and 0,97 kJ/g in summer and winter respectively. If we assume that squirrels lost the minimum amount of water during the cold-dry winter, flux being closely correlated with the previous three months rainfall, both the winter studies qualify. The average water flux of the two winter periods was 0,037 ml/g body mass.

It is proposed that X. inauris begin and terminate their surface activity based on their appraisal of environmental conditions, on external and internal dynamic states (e.g. nutritional requirements, food density) and on experience of their home-area.

X. inauris were always acutely alert even when relaxing, their eyes being situated on the sides of their heads give them vision in all directions, but overt vigilant stances took place 11,6 % of the daily activity time. Group signals such as tail flicking, freezing behaviour and vocalizing, enhanced escape. The presence of males in the female home area elicited chasing and fighting by the older female. During such encounters sexual chasing, mating, anal and nose sniffing would take place.

No age or sex class differences in home area size could be detected. Squirrels had larger home areas of 7,4 $\pm$ 2,6 ha during winter than during mid-summer (3,85 $\pm$ 0,48 ha). Home range shapes was influenced by the dome-shaped dune topography of the study area.

It is not clear whether or not energy requirements for most winter-active endotherms actually increase during the cold-dry winter months. At 14° C, without nesting material, single animals showed signs of shivering thermogenesis, while huddled groups of two, four and six squirrels could save between 8,9 % and 40,0 % of their energy expenditure respectively.

Little specialization occurred in the gut of X. inauris, but their digesta passage rates were comparable with other monogastric mammals. The large caecum provides flexibility in utilizing different foods in the event of food shortage.

Seasonal annual patterns of water and energy availability differ from year to year in the Kalahari. X. inauris have no choice but to eat fibrous foods in winter, to resort to roots, and take termites. Poor nutritional quality of forage might induce squirrels to move to sites of more plentiful vegetation.

OPSOMMING

Xerus inauris is groot, daglewende, koloniale en plantvretende knaagdiere wat tonnels bewoon. Hul verspreiding in semi-woestyndele met wisselvallige reënval, het vrae oor hul aanpassings vir oorlewing laat ontstaan: Onder hoeveel druk verkeer hierdie eekhorings in 'n omgewing, wat deur die mense, as onvoorspelbaar beskou word?

Plante soos Tribulus terrestris het regdeur die jaar sukkulente blare, stingels, blomme en wortels verskaf. Sulke plantmateriaal was 'n bron van water en proteiene vir X. inauris.

Die sentrale tonnelstelsel word deur al die lede van die groep vir skuiling gedurende die dag en nag gebruik. Al die ander tonnels in die tuisgebied word op 'n ad hoc basis deur individuele lede gebruik om roofdiere en uiterste somertemperature te ontduik. Enige omgewingstemperature buite die termo-neutrale sone van 29 tot 33 °C het 'n negatiewe effek op hul metabolisme gehad. Terwyl die omgewingstemperature dus gewissel het, was dit vir hulle voordelig om in tonnelstelsels te rus waar konstante temperature geheers het.

Dit is nie duidelik of die energiebehoeftes van die meerderheid endotermiese diere wat in die winter aktief is toeneem nie. Individuele eekhorings het by 14 °C , sonder nesmateriaal, begin bewe, terwyl groepe van twee, vier en ses eekhorings wat gebondel het, 8,9 - 40 % energie bespaar het.

Daar word voorgestel dat die tydsduur wat X. inauris aan bo-grondse aktiwiteite bestee, afhang van omgewingsfaktore, eksterne en interne dinamiese toestande (bv. voedingsbehoeftes en voedseldigtheid) en van hul kennis van die tuisgebied.

X. inauris was altyd baie waaksaam, selfs tydens ontspanning. Hul oë is aan die laterale kante van hul koppe gelee, wat 'n wye gesigsveld tot gevolg het.

Waaksaamheid het 11,6 % van hul daaglikse aktiewe tyd in beslag geneem. Wanneer gevaar dreig, word ander lede van die groep gewaarsku deur stertseine, vriesgedrag en alarmroepe. Die teenwoordigheid van mannetjies in die tuisgebied van die wyfies het 'n gejaag en bakleiery deur die ouer wyfie ontlok. Gedurende sulke ontmoetings het seksuele gedrag en paring plaasgevind. Geen ouderdoms- of geslagsverskille is waargeneem in tuisgebiede wat verskil in grootte nie. Eekhorings het groter tuisgebiede gedurende die winter (7,4 $\pm$ 2,6 ha) as gedurende middel-somer (3,85 $\pm$ 0,48 ha) gehad. Die duine rankskikking of topografie van die studie area het die woongebiede van eekhorings bepaal.

Weinig spesialisasie is in die spysverteringskanaal van die eekhorings waargeneem. Indien skielike habitat- en klimaatsveranderinge herbivore in die gesig staar, beskik hulle oor die vermoë om sekere gedeeltes van hulle spysverteringskanaal aan te pas. Die tyd wat dit neem vir voedsel om deur die spysverteringskanaal van X. inauris te gaan kan vergelyk word met die van ander monogastriese diere. Die groot caecum is 'n aanpassing om verskillende voedselsoorte te kan benut in tye van voedselskaarstes.

Minimale rus-onderhoudende energie vir X. inauris was onderskeidelik 0,84 kJ/g en 0,97 kJ/g gedurende die somer en winter. Die resultate toon dat eekhorings gedurende die koue droë winter maande die minste waterverlies toon en dat die wateromset afhang van die vorige drie maande se reenval. Die gemiddelde wateromset vir die twee winterperiodes was 0,037 ml/g liggaamsmassa.

Seisoenale patrone in die water- en energiebeskikbaarheid in die Kalahari verskil jaarliks. X. inauris moet dus noodwendig voedsel met hoë veselinhoud, wortels en moontlik ook insekte gedurende die winter inneem. Swak voedselkwaliteit mag eekhorings dwing om te verskuif na gebiede waar plantegroei meer volop is.

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Appendix 1. Plant species, percentage cover and rainfall at 'Rodent Hill' measured from Sept 1987 till October 1988.

SPECIES	MONTHS							
	09	11	12	02	04	06	08	10
NO VEGETATION	78,9	75,0	68,9	58,7	53,7	60,5	70,0	68,0
E.lehmanianna	1,5	0,9	0,5	1,5	4,2	3,0		2,0
S.kalaharensis	0,6	1,4	5,0	8,9	10,6	9,4	8,2	10,0
A. glaucum					0,4			
S. amabilis	0,6	0,5	0,5	0,7	0,8	0,8	0,8	0,8
S.ciliata	0,7	0,8	1,0	0,5	1,5	1,0		0,5
G.flava	0,2	0,2	0,3	0,2	0.3	0,3	0,2	0,3
A. erioloba	0,6	0,6	0,5	0,5	0,5	0,5	0,6	0,5
B. albitrunca	0,2	0,2	0,2	0,2	0,2	0,2	0,2	0,2
A.haematoxylo	0,4	0,3	0,3	0,3	0,4	0,3	0,4	0,4
R. trichotomum	0,2	0,2	0,2	0,2	0,2	0,2	0,2	0,2
A. mellifera	0,2	0,2	0,3	0,2	0,2	0,2	0,2	0,2
Helichrysum						0,4	4,5	2,5
Limeum	2,2	7,6	16,2	16,4	9,5	4,2		4,2
T. terrestris	4,6	1,8	1,0	2,7	3,3	5,2	5,2	5,1
Pentzia	1,0	1,0	0,7		0,5	0,3		
Requina	2,0	2,0	0,3					
Sesamum	0,3	1,4	2,0	2,8	3,6	2,0		1,5
Herbstaedia			1,5	2,0	3,5	2,0		
Citrillus		0,1	0,3	2,9	4,2	3,4	3,0	2,1
Cassia				0,5	2,2			
Moribund	5,8	5,5	0,5	0,5	0,0	5,0	6,8	5,0
TOTAL COVER %	16,0	24,5	30,6	41,2	46,2	33,5	23,2	26,9
mm RAINFALL	2	53	11	119	128			6,5